The Life History of the Snow Crab,
Chionoecetes opilio:
A Literature Review

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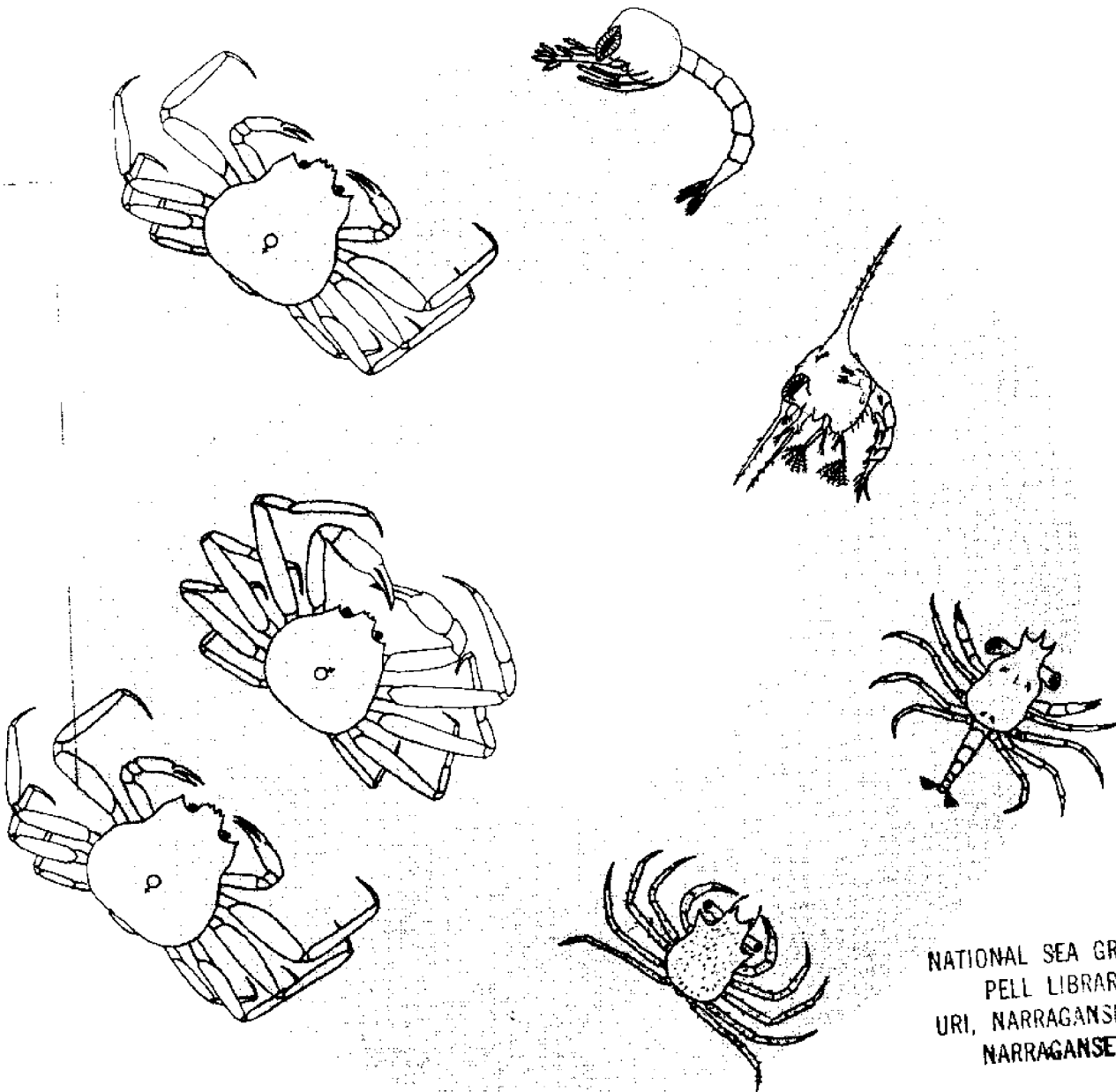
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a Literature Review

by

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ACKNOWLEDGMENTS

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ABSTRACT

The eggs of *Chionoecetes opilio* measure 0.5 to 1.1 mm in diameter and hatch into prezoea which are less than 3 mm total length. Prezoea escape from the egg mass beneath the female's abdomen and begin their upward migration from depths as great as 350 meters. Laboratory rearing experiments indicate that the pre-zoea undergo metamorphosis to zoea within hours, or at most days, after hatching. Prezoea and zoea are present in the water column between the months of February and July. Maximum numbers of larvae are found early in southerly waters (in the Sea of Japan) and late in the Gulf of St. Lawrence and in the Bering Sea. Within one month the zoea I molts to a stage II zoea. The greatest concentrations of both zoeal stages are found within the upper 10 meters of the water column. Total body length (4 to 5 mm in stage I and 6 to 7 mm in stage II) and the number of setae on most appendages increases from the first to the second stage zoea.

Metamorphosis to megalops occurs within a month after the emergence of zoea II. Three rostral spines, a shield-shaped carapace, and five pereiopods give the megalops its first crab-like appearance. This small larva, which measures 6 to 7 mm, emerges from the zoea II in near-surface waters. Generally megalops are collected from April through February although this period varies con-siderably with geographic location. Estimates of duration for the megalops range from one to ten months. During this time span the larva migrates from the surface toward the sea floor and, either shortly before or upon reaching the benthos, it metamorphoses into a first instar.

Instars are the first forms that possess features of true crabs. Following the third instar stage, immature males and females can be differentiated. Female crabs pass through at least 7 and possibly as many as 12 instars before a final molt to maturity. Male crabs undergo at least 7 and possibly as many as 10 instar molts, emerge as sexually mature adults, and continue to molt either annually or biannually. Carapace widths of instar I crabs of both sexes are about 4.5 mm. An approximate 30 percent increase in carapace width is gained at each successive molt. Estimates of instar longevity in different locations vary but it is likely that either the first three or four instars are completed in twelve months. Instar V requires six months and the remaining instars represent six to twelve months apiece in the life of the crab. In the Sea of Japan, instar stages I through VI occur in the depth zone 300 to 350 meters. Instars VII and VIII rapidly disperse within a depth zone of 200 to 400 meters. The last two instar stages are found between 200 and 250 meters.

Evidence indicates that the molt to maturity is the final molt in the life cycle of female *C. opilio*. In the Sea of Japan, the emerging adult females have carapace widths of 60 to 75 mm and are found at 200 to 350 meter depths with greatest numbers at 200 to 250 meters. Most males, however, with carapace widths exceeding 90 mm are found between 275 and 400 meters. The larger males

undertake seasonal migrations which bring them in contact with female crabs that are molting to maturity. Mating occurs after the females molt. Although females are reported to mate only during the soft-carapace phase immediately following the molt to maturity, they can produce fertile egg clutches for at least the next two years because viable sperm are stored within their seminal receptacles for that length of time. In spring, February through April, each mature female extrudes between 5,500 and 150,000 eggs [Sea of Japan (Ito, 1963); 20,000 to 140,000 eggs in Gulf of St. Lawrence (Watson, 1969)] which adhere to the pleiopods and are covered by the abdomen. Fertile eggs of multiparous females hatch within 12 months; however, in some locations such as the Sea of Japan, the eggs of primiparous females may require 18 months for complete development. Maximum estimates of total life span for *Chionoecetes opilio* are 11 to 12 years for females and 14 to 16 years for males.

INTRODUCTION

Chionoecetes opilio (O. Fabricius), a commercially important brachyuran, consists of two forms: *C. opilio* (Fabricius) and *C. opilio elongatus* (Rathbun).[1] Both forms inhabit the Sea of Japan; however, *C. opilio* also occurs in the Bering Sea, Arctic Ocean, and the North Atlantic as far south as Casco Bay, Maine (Garth, 1958). Due to its wide geographic distribution, relatively high abundance, palatability, and marketability, *C. opilio* has been exploited by Russian, Japanese, and Canadian fishermen. It has also been the subject of numerous scientific studies. However, the life history of *C. opilio* has not been described in a singular exhaustive account. A review of the literature reveals that this topic has been considered only by examination of separate stages of the life cycle. In this paper an attempt has been made to combine the pieces to provide a tentative but continuous picture of the entire life cycle based on the available literature. For purposes of comparison, information has been presented from two widely separated areas -- the Sea of Japan and the Gulf of St. Lawrence (Figure 1).

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[1] According to Nishimura and Mizusawa (1969) a hybrid form, resulting from natural interbreeding of *C. opilio* and *C. japonicus*, also exists. These hybrids are intermediate between the parental types in morphological, physiological, and ecological characteristics. A second hybrid form, with characteristics intermediate between *C opilio* and *C. bairdi* has been described by Karinen and Hoopes (1971).

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Part I

Reproduction and Larval Stages

A. Spawning and Egg Development

Sexes are separate and sexual dimorphism is apparent in the adults. Mating
occurs during September and October in the Sea of Japan and between May and
July in the Gulf of St. Lawrence for animals spawning for the first time.
Males mate with females just after the latter undergo a terminal molt to
maturity (Ito, 1963b; Watson, 1972). Spermatazoa are stored in the female's
seminal receptacles which are connected to the oviduct (Hartnoll, 1968).
Primary spawners ovulate immediately after mating. Sperm attach to the ova
as the latter pass by the seminal receptacles and move down the oviduct
(Watson, 1969). Following the first ovulation, a female's ovaries remain
immature for six months (Ito, 1967). During the succeeding spring the
ovaries of primiparous spawners begin to mature at approximately the same
time and rate as those of multiparous females. Ovary maturation begins
during March and April and reaches a peak during February and March of the
following year. Multiparous spawning occurs during the months of February,
March, and April. The cycle of ovary maturation requires one and one-half
years for primiparous females and one year for multiparous spawners (Ito,
1967). Multiparous females ovulate within days of the hatching of the
previous year's eggs.

Fertilized, extruded eggs attach to the abdominal appendages thereby forming
the egg mass (Watson, 1969). Egg size for both Bering Sea and Gulf of St.
Lawrence crabs is quite uniform with individual maximum diameter of preserved
eggs in the range of 0.49 to 0.66 mm (Bering Sea) and 0.56 to 0.75 mm (Gulf
of St. Lawrence) (Haynes, et al., 1976). Gulf of St. Lawrence primiparous
female *C. opilio* carry more eggs for a given carapace width than their
counterparts in the southeastern Bering Sea (Haynes, et al., 1976). Un-
fortunately, females of mixed spawning history from the Bering Sea were not
studied. Apparent geographic differences in the fecundity may be due to
differences in the success of egg attachment between first- and second- or
third-time spawners.

In the waters off Gaspé (Quebec), berried females are most abundant at
depths between 50 and 79 fathoms (Table 1). Japanese authors do not mention
migration of berried females. These animals must remain within the normal
depth distribution of non-berried females.

A stage by stage description of the development of the eggs of *C. opilio*,
published by Ito (1967), is provided in Table 2.

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This appears to be an accurate description of the various developmental stages of eggs in both the Sea of Japan and the Gulf of St. Lawrence. Eggs of primary spawners remain attached to the abdominal appendages for about 12 months without developing eyes (Ito, 1967). Eggs of both primiparous and multiparous spawners enter the stages of early and intermediate eye formation from September to February (Table 3).[1] Development proceeds into the later eye-forming stage from January to March. Hatching occurs from February to April in the Sea of Japan (Ito, 1967) with a peak in March (Table 4).

Kurata (1963) found that farther north, in the Okhotsk Sea, hatching occurs at a later date from May to July. The time of hatching is still later along the Pacific Coast of Japan, where zoea do not appear until August and September (Kurata, 1963). In the Gulf of St. Lawrence, hatching is reported to occur from late April to June (Watson, 1969) and during May and early June (Powles, 1966).

Ito (1967) suggests that the developmental tempo of the eggs of primary spawners is checked to a great extent during early stages of development. However, he did not attempt to explain the mechanism which is responsible for the delay.

B.   Larval Stages

C. opilio has a fairly long larval life when compared with other crabs (Ito, 1967). The larva emerges from the egg as a prezoea covered by an embryonic cuticle (Figure 2). Total body length of the prezoea measures approximately 2.48 mm (Haynes, 1973). Kon (1967) provides a brief description:

> "There are no spines on the carapace. First antenna is tipped by a long and a short plumose seta. Second antenna has a short process and an exopodite bearing 4 plumose setae on each side. The telson is bifurcated posteriorly and has seven spines on each side. The first and fourth spines from the outside are smooth, while the rest of the spines are plumose. The fourth spine is very small."

Kuwatani, et al. (1971) determined the duration of the prezoea stage in vitro. Egg masses which had already begun hatching were removed from females and shaken in sea water in Petri dishes. The emerging prezoea were transferred to new dishes and maintained at about 5°C in a thermostatic box. The number of individuals which metamorphosed to first stage zoea was counted at 20 minute intervals after hatching (Figure 3 and Table 5). Approximately half of the total number of prezoea metamorphosed to zoea within 40 minutes after hatching. Most underwent metamorphosis within 20 to 40 minutes after hatching. It is important, as the authors note, to bear in mind the fact that hatching may be promoted by stimulation during shaking. Effects of varying temperature on duration of metamorphosis were not studied.

The prezoea casts its skin within 40 to 60 minutes after hatching (Kon, 1967 and 1970). Exuviation proceeds in the following order:

1)   unfolding of the maxillipedes (20 to 30 minutes after hatching);

2)   flick up of the lateral and dorsal spines;

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[1] Eye spots appear in the eggs carried by females in the water off Gaspé, Quebec, during September but are most numerous during the winter months (Watson, 1969).

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3) molting of the cephalothorax, first and second antennae and maxillipedes; and

4) stretching out of the rostral spine and the sinous process, molting of the abdomen and telson.

The newly emerged larval form is that of a zoea (Figure 4) - a description of its morphological features is provided in Appendix I.

The seasons of appearance of larval stages are listed in Table 4. Collections made by Kurata (1963), along the Sea of Japan coast of Hokkaido contained zoea during the months of March through June[1] (1960 - 1962). Zoea appeared in collections along the coast of the Okhotsk Sea during May, June, and July. Along the Pacific coast of Japan, zoea were collected in August and September.

The foregoing specimens were all captured at the surface. However, during March, 1967, Ito caught larvae at the surface and at a depth of 10 meters in the Sea of Japan off Sado. Only a few larvae were collected at the surface while many more of the zoea I were taken at a depth of 10 meters (Ito, 1968).

Differences in the time of appearance of the planktonic larvae seem to be due to the differences in environmental conditions of the areas surveyed. Kon (1970) conducted laboratory rearing experiments in an attempt to define the temperature requirements of *C. opilio*. He observed that if the rearing conditions such as the quantity and quality of food or light are satisfactory, a relationship is established between the time required for each molting period and the mean water temperature or the cumulative water temperature during the period (Table 6). The following paragraphs outline Kon's experimental results.

In the Sea of Japan, zoea I appear in plankton collections when the surface temperature is 4 to $16^{o}C$, second stage zoea appear at 4 to $17^{o}C$, and megalops at 1 to $17^{o}C$. Large numbers of specimens are caught when the surface temperature ranges are 4 to $7^{o}C$, 4 to $14^{o}C$, and 10 to $11^{o}C$ respectively for zoea I, zoea II, and megalops.[2] Rearing experiments show that survival is possible only at temperatures less than $18^{o}C$ and suitable temperature ranges appear to be 7 to $15^{o}C$ for the zoeal stages and 12 to $17^{o}C$ for the megalops stage.

Kon raised groups of zoea I in separate vessels containing sea water of different, but overlapping, temperature ranges between 4.1 and $19.8^{o}C$ (Tables 6 and 7). At the highest temperature range (18.9 to $19.8^{o}C$) all of the young died within 14 to 15 days (cumulative water temperature of 272.6 to $291.4^{o}C$ days) without molting to zoea II. The number of days required for molting (in the successful groups) was 10 to 53 and the time required decreased with a rise in temperature. Cumulative water temperature of the successful molts was in

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1   Fukataki (1965) agrees with this schedule of occurrence of zoea in the Sea of Japan. He captured first stage zoea in March, April, and May (1964 and 1965) and second stage zoea from March through June. During the same years, Ito, Kasahara, and Ikehara (1967) collected zoea in April and May from the southwest area of the Sea of Japan.

2   Takeuchi (1969) described the water temperature range of zoea I megalops as -1.1 to $10.4^{o}C$ off northeastern Hokkaido.

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the range 215.4 to 254.7°C days. The relationship between number of days re-
quired for molting (Y) and average water temperature (X) was:

$$Y = (300.89) \div (X^{1.117})$$

The optimum temperature (yielding a success of 52 to 57%) for molting to
zoea II ranged from 7.9 to 12.9°C (average water temperature 9.6°C). Lower
molting success (36.5 to 37.0%) was obtained in temperature ranges 10.0 to
17.1°C, 15.5 to 17.0°C, and 16.5 to 18.8°C. The poorest molting success (10 to
14%) was obtained in the temperature range 4.1 to 9.6°C. Individuals reared
at 4.1 to 9.6°C were generally lethargic.

Molting to megalops occurred after 11 to 61 days. As in the case of zoea I,
the intermolt period decreased as the temperature increased. During the zoea
II stage, the relationship between time required for molting (Y) and
average temperature (X) was:

$$Y = (367.45) \div (X^{1.1619})$$

Cumulative temperatures in this experiment ranged from 217.3 to 299.3°C days.
Greatest molting success (53 to 60%) to the megalops stage was obtained in
water which ranged from 7.1 to 10.7°C. Lower molting successes, listed in
decreasing order, were achieved in the following temperature ranges: 12.1 to
14.7°C; 15.0 to 16.6°C; 4.2 to 7.2°C; and 17.5 to 18.9°C. Many larvae died
during the molt at water temperatures of 4.2 to 7.2°C. Excluding the two least
optimal temperature ranges, it appears that within the range of 7.1 to 16.6°C
the molting success decreases with rise in temperature.

Specific gravity of water apparently has some effect upon the survival of
the zoea (Figures 5 and 6). Kon (1973) recorded a minimum intermolt period
for zoea I and zoea II in water with a specific gravity of 1.020 to 1.022.
Survival was over 70% for zoea I held in water of specific gravity 1.022 to
1.027. An identical survival value was obtained for zoea II in water of
specific gravity 1.019 to 1.026. When reared in water of specific gravity
1.012 or less, most of the first stage zoea failed to molt completely and
those that succeeded died within a few days.

Kon (1970) raised 69 megalops in water of three overlapping temperature
ranges between 8.5°C and 17.4°C. For the ten surviving megalops, the inter-
molt period varied from 26 to 30 days. Kon concluded that it was impossible
to make a valid statement concerning the relationship between the length of
this larval stage and the water temperature. The greatest molting success
(18 to 29%) was obtained at 12.5 to 15.0°C and 12.7 to 17.4°C. The cumulative
water temperature ranged between 261.7 and 442.1°C days for megalops.

Seasonal occurrence of megalops in waters off Japan varies greatly from
April to the following February (Tables 5 and 8).

C. Larval Duration

Upon the basis of rearing experiments (such as those mentioned earlier), as
well as the presence of larvae in plankton collections, longevity of each larval
stage is determined (Appendix II). Estimates of length of planktonic larval
life are listed in Table 9 in an order of increasing longevity.

There are considerable differences in the estimates of the length of larval life (particularly of the important megalops stage). The megalops stage represents a major transition in the life style of the crab. For it is at this time that the larva moves from the surface water (with higher temperature) to much deeper water (300 to 400 meters) with lower temperatures. A behavioral change also occurs in the crab. Larval life is typified by a free-swimming planktonic existence. Instar life brings the animal in contact with the benthic environment and a different complement of predator and prey organisms. The speed with which this relocation occurs has not been determined, yet it is one of two main sources of discrepancies in the estimation of the total length of the larval period.

Another period of questionable length is the time required for the newly hatched larvae to migrate from depth at the site of hatching (240 to 260 meters in the Sea of Japan) to the surface. Ito and Kon have taken opposite viewpoints on this subject (Appendix II). Ito (1970) believes that the move to deeper water, by the megalops, is a slow process and that the megalops spend much of their lives at 300 to 400 meters. Kon (1970), on the other hand, believes that both the upward migration by the newly hatched prezoea and the downward migration by the megalops are rapid and that low temperatures are therefore encountered for only a brief while. If the latter hypothesis is correct, the temperature effect on these stages of larval development may be insignificant.

D. Geographic and Bathymetric Distribution of Larvae

The *Chionoecetes* larvae are widespread throughout the Sea of Japan in near surface waters (Kurata, 1963; Fukataki, 1965b: Ito, et al., 1967) and in some area centers of larval distribution are usually far from the main commercial fishing grounds (Ito, 1968). Since the larvae of *C. opilio* and *C. japonicus* have not been satisfactorily differentiated (Fukataki, 1965a), plankton collections have probably included larvae of both species[1]. Thus it is impossible to discuss the distribution of either species in detail. It is presumed that the young of both species settle to the bottom (after the megalops stage) as instars. Ito (1970) proposes that a sharp rise in the temperature of the surface waters during June (Figure 7) triggers the migration of megalops into deeper waters.

Instar I crabs occupy depths of 275 to 400 meters. Due to the presence of early instars in deep water, Ito (1968) suggests that the megalops end their migration and undergo the molt to the instar I stage at depths of approximately 300 to 400 meters.

This molt occurs between October and February in the Sea of Japan (Ito, 1968). The months of August to October encompass the season of the molt from megalops to first instar in the Gulf of St. Lawrence (Watson, 1969). Average carapace width of the megalops is 2.2 mm (Kurata, 1963); carapace width of the first instar is in the range 2.4 to 3.4 mm (Ito, 1968).

Concerning larval life history Kon (1970) and Ito (1968) concluded respectively:

"The period of occurrence of larvae of the tanner crab genus differs depending on the region in the Japan Sea. It will be necessary in

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[1] Motoh (1976) recently distinguished the zoea and megalops of these species (Appendix I).

the future to obtain sufficient data on the depth at which the larvae are found and the environmental temperature, and at the same time to distinguish the larvae of *Chionoecetes opilio* from those of *C. japonicus*. It will also be necessary to improve the results of rearing experiments of megalops and to complete the knowledge of the ecology of this period."

"It is problematic to discuss the time of appearance of larvae in detail because it is based on the collection at and near the surface and there is no distinction between *C. japonicus* larvae (and those of *C. opilio*). In the case of *C. opilio* the question still remains of the difference in the water temperature between the cultural experiment and the natural habitat."

PART II

Juvenile and Adult Life History

A. Significance of the Instar

In appearance, the instar is a miniature version of the adult (Figures 8 and
9 and Appendix I). Before instars reach a carapace width of 6 mm, the sexes
are indistinguishable (Ito, 1968). During instar life many changes will occur
in size, in relative dimensions of the body parts, and in the distributions on
the sea floor. These changes, and others, are discussed in this section.

B. Age and Growth

Several researchers (Kon, Watson, Ito, and Sinoda - to name a few) have separately
approached the questions: How much time elapses during each stage of develop-
ment? What is the longevity of *C. opilio?* During its entire life span, a female
C. opilio will undergo at least eleven molts[1] (1 prezoea, 2 zoea, 1 megalops, and
at least 7 instar molts -- some females may undergo as many as 9 instar molts)[2],
Tables 8 and 10. The male will undergo at least 13 molts (1 prezoea, 2 zoea,
1 megalops, 7 instar and at least 2 adult molts) during its complete lifetime.
Tables 11 and 12 compare the available estimates of age at different stages of
development. As discussed earlier, it is calculated that the total larval life
accounts for a period of 3 to 10 months depending upon the environmental con-
ditions and the author.

Instar stages are not of equal duration because the intermolt period decreases
with age. Ito (1970) assigns a summed duration of one year to instar stages
I, II, III, and IV; 16 months to instar stage V; and approximately 12 months to
each stage after and including instar VI. Kon (1969) and Watson (1969) each
believe that early instar development is a little less rapid. They attribute
one year to instar stages I, II, and III; six months each to instar stages IV

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[1]   Ito does not count the prezoeal molt as a true molt; whereas it is counted
     here as a definite molt in the life cycle.

[2]   Small numbers of female *C. opilio* were collected with carapace widths ex-
     ceeding the upper limit of the range of carapace widths for the instar
     VIII stage (Ito, 1970). Ito postulated that some females may undergo the
     molt to maturity after an instar IX stage.

through IX[1]; and one year (12 months) to each stage after instar IX, although
a bi-annual molting period is quite possible beyond the adult II stage.[2] [3] [4]

The greatest difference between the growth of opposite sexes of *C. opilio* is
that the females experience a terminal molt to maturity. With only rare ex-
ceptions (one such case is described by Ito and Kobayashi, 1967), females
simply cease to molt and grow following their first ovulation (Figure 10).
Males, on the other hand, continue to molt and grow after sexual maturity is
reached.

In order to estimate longevity one must refer to size records for a species
and, having determined the largest size mode, attempt to age on the basis of
age-size models. Ito (1970) mentions two very large males, one 174 mm and the
other 167 mm carapace width, which were donated to the temple of the Diety
Kotohira at Kasumi. If one assumes: (1) that Ito (1970) has correctly
estimated an age of 12.5 years for males with carapace width of 138 mm; and
(2) that crabs larger than 100 mm molt once every two years, then the two large
specimens could be 14 to 16 years of age.

Several authors warn that age-growth models remain unresolved for the oldest
adult males due to the close clustering of carapace width ranges of different
molting groups (Figure 11b). There is much overlap between molting groups
and the divisions between stages are presently hypothetical.

Females are difficult to age after they have reached maturity due to the
cessation of their growth at that time. Little is mentioned concerning the
maximum age of females and the only available estimates are those of Tanino
and Ito (1968) and Kobayashi (1965). The method utilized in both studies was
a mark-recapture technique. The maximum periods of elapsed time between
marking and recapture were 620 days (Tanino and Ito, 1968) and 458 days
(Kobayashi, 1965). With these results in mind, Ito (1970) concludes that
females live for 3 to 4 years as mature crabs (Table 10). His estimation for
the longevity of female *Chionoecetes opilio* is 9.5 to 12.5 years (6.5 to 8.5
years as immature crabs plus 3 to 4 years of adult life). This matter has
neither been concluded nor thoroughly studied.

Seasonality of maximum molting activity varies with successive developmental
stages. However, the seasonality of molting activity is a phenomenon
which is intimately associated with duration of each of the molting stages.

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[1]   A duration of six months for each of these stages does not seem logical be-
      cause it would entail a sudden acceleration in the growth rate. Supposedly
      the growth rate would remain at this accelerated level for three years then
      decrease. The growth data presented later in this paper does not appear
      to support such a pattern of accelerated growth.

[2]   For male crabs with carapace widths of 100 mm (adult II stage and higher),
      Watson (1969) believes that a bi-annual molting period is more likely.

[3]   After mark-recapture studies of *C. opilio* in Wakasa Bay, Niwa (1967) con-
      cluded that adult males--size range not cross-referenced by Ito (1970)--
      require at least two years between each molt.

[4]   Not to be overlooked are the mark-recapture studies by Kobayashi (1965)
      which seem to indicate that adult males molt once each year.

On the basis of the frequency of occurrence of first through third stage instars in the stomachs of the zoarcid fish, *Petroschmidtia toyamaensis*, and the results of trawl catches (instar IV - adults), Ito (1970) constructed the time schedule of presence and peak abundance for each of the instar and adult stages listed in Table 13.

Since the occurrence of instars I, II, and III was determined from the results of analyses of the stomachs of *P. toyamaensis*, the accuracy of statements concerning these stages is questionable and the need for additional study is obvious. The effects which geographic location and environmental variables have upon the duration and seasonality of different developmental stages also warrant additional study.

Changes in body dimensions at each stage in the life of *C. opilio* have been more thoroughly established. The step-wise growth pattern which is typical of all crustaceans has been measured in *C. opilio* by several researchers (Table 10). Each of the studies examines only a section of the total growth history of the organism; therefore, in order to construct a tentative model for growth (Tables 14-16), I combined the results of different studies and averaged the values of mode of carapace width for each of the molting groups. As mentioned earlier, the growth rate and carapace width for adult males remain highly speculative and it would be improper to offer firm assurance that the carapace width modes greater than 90 mm are correctly identified. In increasing size, the carapace width modes (beginning with the prezoea) are: <1; <1.2; 1.5; 3.0; 4.5; 6.6; 9.5; 13.5; 19.5 (female = 27.6); 37.3 (female = 37.8); 49.2 (female = 49.6); 63.9 (female = 65.0); 77.7 (female = 75.1); 91.4 (female = 84.3); 111.2; and 132.4 mm.

Ito (1970) characterizes the carapace width distribution of this species as follows:

> "Males and females of the same molting stage, for all of the immature stages as well as the adult I stage, coincide very closely in mode of carapace width and carapace width range where collections contained large numbers of crabs."

Figures 11 to 14 and Tables 10 and 17 to 21 illustrate carapace width modes and frequencies.

Growth is also frequently expressed in terms of percentage increase in carapace width per molt. Using the values for mode of carapace width published by Sinoda (1968), Kon, et al. (1968), and Ito (1970), the percentage increase is calculated for each molting stage in each study (Table 21).

The greatest increments in growth occur during the megalops and instar periods with percent increase values ranging from 25 to 43 percent (Miller and Watson, 1976). The range of values of percent increase dropped at the molt to maturity to approximately 18.4 percent for males and 14.8 percent for females (Miller and Watson, 1976) (Figure 15). All succeeding molts for mature males entailed approximately an 18.4 percent increase in carapace width per molt. Thus there

is a trend that percent carapace width increase per molt decreases with the approach of maturity but remains at a relatively constant value during all adult molts.

Numerous growth equations (Tables 22 and 23) have been derived from morphometric measurements. The proportionate changes in body dimensions which the equations describe are: carapace width (post-molt)/carapace width (pre-molt) (Figures 16 to 20); carapace length/carapace width; body weight/carapace width (Figures 21 and 22); meropodite length/carapace width (Figure 23 and Tables 24 and 25); claw length/carapace width (Figure 24); merus width/merus length; abdominal segment width/carapace width (Figures 25 and 26); and distance between orbits/ carapace width (Figure 27). The method which has been most frequently applied in growth studies of *C. opilio* is Hiatt's graphical analysis (used by Kon, Niwa and Yamaka (1968), Kurata (1960), and Ito (1970)). According to this technique, the post-molt carapace width (L_{n+1}) is plotted on the vertical axis while the pre-molt carapace width (L_n) is plotted on the horizontal axis (Figures 18 and 19). In this manner *Chionoecetes opilio*'s growth is described by a straight line equation of the form:

$$L_{n+1} = a L_n + b, \text{ where } a = \text{slope of the line (coefficient of growth)}$$
$$b = x - \text{axis intercept}$$

The linear equations which were obtained by the least squares method are listed in Table 23. Quite clearly, the growth equations demonstrate a nearly equal growth rate between immature male and immature female crabs. This similarity holds true for both carapace length/carapace width and for the body weight/carapace width relationship (see Kanno's equations Table 22).

However, as the instars of both sexes approach maturity, distinct breaks may be seen in five of the plotted growth lines (which express the size relationship between different body dimensions). These include the following:

(1) Carapace width/carapace length - There is a jump in the position of the growth line followed by a decrease in the slope.

(2) Width of 5th abdominal segment/carapace width - A jump in the position of the line occurs at 50 mm carapace width and is followed by a decrease in its slope. This only applies to females (Figures 25 and 26).

(3) Claw length/carapace width - Increase in position and slope of the growth line commences at 60-70 mm in males (Figure 24).

(4) Claw breadth/carapace width - Increase in position and slope of the growth line commences at 60-70 mm in males (Figure 24).

(5) Weight of the vas deferens/carapace width - A plateau appears in the slope of the line at 70-80 mm carapace width. (Males only - Figure 28).

The approach of maturity is a time of considerable morphological and physiological change. Between the 14th and 15th molting stages, the males' and females' co-efficients of growth for post-molt carapace width/pre-molt carapace width have values less than one. At this time, large amounts of energy are being directed to gonadal

growth rather than somatic growth. In addition, secondary sex characteristics are manifested as the abdomen of the female becomes wider and the claws of the male become more robust - longer and wider. All of the changes are triggered by hormonal activity.

The androgenic gland is responsible for producing a hormone or hormones (believed to be protein or peptide) which determines all the primary and secondary sexual characters of the male (Charniaux - Cotton, 1954). The ovary is responsible for the production of hormones determining both temporary and permanent sexual characters of the female (Charmiaux - Cotton, 1954).

The Y-organ (or ventral gland) produces a hormone (or hormones) which triggers the initial stages of gonad development as well as limb bud development and initiation of proecdysis (Demenusy, 1958 and Arvey, et al., 1956). In turn, the functions of the Y-organ are under the inhibitory effect of the X-organ (or sinus gland) which possesses the following additional hormonal activities: (1) control of sugar metabolism; (2) control of metabolic rate; (3) control of pigment dispersion; (4) control of body protein metabolism; (5) control of water metabolism; and (6) control of heart rate (Lockwood, 1967). Lockwood (1967) suggests that terminal anecdysis may arise in one of two ways: "Either, as in *Carcinus*, there is a continuous release of inhibitor by the sinus gland so that the Y-organ can never secrete the molting hormone, or alternatively, as in *Maia*, the Y-organ itself may regress."

Previous to the instar X stage, males and females molt at approximately the same time and the same size (Ito, 1970 - Figures 29 and 30). During the instar X stage a difference appears between males and females in the months of peak molting activity. Females undergo the molt to maturity between September and October in the Sea of Japan (Figures 29 and 30) and between June and November in the Gulf of St. Lawrence (Figure 31). In the case of males, the molt to maturity (and all subsequent molts) occurs between October and December in the Sea of Japan and between May and September in the Gulf of St. Lawrence.

Considering the comparative size of male and female crabs in the last instar stage, Ito (1970) found a difference in the total range of carapace widths. The carapace widths of females covered the range 52-79 mm; while males of the same stage measured 52-74 mm in carapace width. The range of carapace widths of mature female crabs is 54-92 mm. A small number of females exceed the upper limit of this range and Ito (1970) suggested that there may be an instar XII. The mature males of *Chionoecetes opilio* have carapace widths in the range 66-96 mm (during the adult I stage) with a mode at 81-82 mm.

Maturation occurs at a smaller size among the *C. opilio* of the Gulf of St. Lawrence, (Tables 26 and 27).

Watson (1969) observed two indisputable signs of maturity among female *C. opilio* at a carapace width of 50 mm:

(1) Fifty percent of the females of this size carried eggs or empty egg cases (Figures 32 and 33).

(2) When the maximum width of the abdomen (segment 5) was plotted against carapace width, a distinct break occurred at 50 mm carapace width (Figure 25).

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For male crabs, Watson (1969) found that claw length and breadth plotted against carapace width (Figure 24) show distinct breaks at 55 to 65 mm carapace width.[1] After examining 30 crabs, he observed that when weight of the vas deferens was plotted against carapace width the mature condition apparently was attained at 55 to 65 mm (Figure 28). Withstanding individual differences, it appears that most female *C. opilio* mature at approximately 75 mm carapace width in the Sea of Japan (Figure 34) and at approximately 50 mm carapace width in the Gulf of St. Lawrence. Most males are mature at approximately 73 mm carapace width in the Sea of Japan and at approximately 57 mm in the Gulf of St. Lawrence.

Estimates of age at maturity vary and this should be no surprise. If growth rates show inter-regional variation, it is reasonable to expect that maturation rates would also vary. Such inter-regional variation is noted for crabs from the Sea of Japan and from the Gulf of St. Lawrence (Table 10). Females are believed to mature at an age of 6 to 8 1/2 years in the Sea of Japan and at 5 to 5 1/2 years (carapace width 50 to 60 mm) in the Gulf of St. Lawrence. Maturity is attained by males at an age of 5 1/2 to 7 1/2 years in the Sea of Japan and at 5 1/2 years in the Gulf of St. Lawrence.

C. Carapace Hardness

Previous to ecdysis a new cuticle partially forms below the existing exoskeleton (Table 28) resulting in the temporary occurrence of "double-carapaced" crabs. Two aspects of the molt cycle are used to time the season of each molting stage; these are:

(1) The appearance of "double-carapaced" crabs (or "futakawagani" in Japanese);

(2) The presence of "soft-shell" or newly molted crabs (called "mizugani" in Japanese) (Table 29).

Ito (1970) caught "soft-shell" immature male and female crabs (in molting stages prior to instar IX) throughout the year - Figures 29 and 30. Peaks can be found in the molting activity of these stages; however, considerable variance in the time of molting of individual crabs produces the year-round occurrence of soft-shell forms. The tendency of monthly average carapace hardness to increase or decrease (Figure 29) follows a seasonal cycle for all molting stages. Furthermore, as was stated earlier the differences in seasonal changes of carapace hardness between immature male and immature female crabs are minor.

The timing of the appearance of double-carapaced crabs is very similar to that of the soft-carapaced crabs (Figure 30). The greatest difference in the abundance of the two forms occurs among the higher molting stage crabs (instar X and larger). In this instance, soft-shell animals are found in greatest abundance about one to two months after the peak in abundance of double-carapaced crabs.

D. Depth Distribution and Migrations, With a Synopsis of Juvenile and Adult Life History

As surface water temperatures rise in June, the megalops of *Chionoecetes opilio* start a downward migration. Just before (or after) settling to the sea floor

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[1] Watson's results agree with those of Kanno (1972) (compare Figure 25 with 26).

in September/October, the megalops molt into first stage instars. The depths at which they settle (300 to 350 m in the Sea of Japan[1]) are determined by such environmental factors as ocean currents and water temperature. Apparently the young instars remain close to their settling depth for 1 1/2 to 2 years. During this time they molt to approximately 19 to 20 mm carapace width (instar VI). Growth to the instar VII and instar VIII stages takes one to two years and during this period many of the juveniles migrate to shallower water (Figures 35 to 39). Due to this migration the overall depth distribution of instar VIII includes depths from 200 to 400 meters with many animals in the 200 to 250 meter zone[2] (Kon, 1969).

Migration into shallower water continues; thus instar IX and instar X crabs (of both sexes) are found concentrated in the depth zone of 200 to 250 meters (Figures 35 to 41). Soon after the molt to the instar X stage, rapid physiological changes commence (Figures 42 to 45). During October and November the ovaries of these females begin maturing. The rate of maturation increases until it reaches a peak in September of the following year (Tables 30 and 31).

Contemporaneously, the carapace is undergoing changes. Beginning at a low value of hardness (1.0) in October, the carapace slowly hardens between January and June until it reaches a maximum hardness of 2.1 to 3.0 (Appendix III).

Following each molt, "...the crab returns to its physiological normal condition and tides over a long rest period between the conclusion of one metecdysis and the beginning of the next proecdysis" (Lockwood, 1967). Softening commences in May or June and continues until September (Figures 46 to 48). The female is now ready for the molt to maturity. In the Gulf of St. Lawrence, Watson (1969) caught no soft-shelled females during his short study; however, new-shelled females were evident from June to October, indicating molting at some earlier time (Figure 31). As primary spawners, females are found at depths of 200 to 250 and 275 to 350 meters (Ito, 1967 - Figures 40 and 41 and Tables 32 and 33). After spawning for the first time, many of the females migrate to deeper water (240 to 260 meters). Multiparous females occasionally migrate to shallower water (Ito, 1967 - Figures 40, 41 and 49).

The early life history of the males closely parallels that of the females. Larval development, size (prezoea through instar IX), distribution, growth rate, molting seasons, and habitat of immature males and females are identical.

Obvious visible differences in the gonad development of male and female crabs do not appear until the instar IX stage. The season of molting of the two sexes first varies during the instar X stage. Males molt from October through December in the Sea of Japan and from June to September in the Gulf of St. Lawrence. Instar X females molt previous to instar X males. The attraction of mature males to primiparous females commences when molting hormone, along with metabolic wastes, is released into the water by the females. Males clasp the females in a "mating

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[1] No published data was available concerning larval settling in the Gulf of St. Lawrence. There was also no available information relevant to migrations by instars.

[2] Ito (1967) reports the peak frequency of instars, considered as a group, to occur at 225 meters off Kasumi.

embrace" until the latter are ready to molt (Watson, 1970). After the new soft-shell adult female has emerged, the male copulates with her. Spermatophores are stored in seminal receptacles of the female. In many cases, the copulation that occurs at the terminal molt to maturity may be the only one in the adult female's life (Ito, 1963b; Watson, 1972). During future ovulations (perhaps two more occur in the following years) the eggs will be fertilized by spermatozoa which have been stored in the seminal receptacles since the original mating (Ito, 1963b; Haynes, et al., 1976).

In the Sea of Japan, mature males remain at depths of 200 to 250 meters until they grow to approximately 90 mm carapace width. They then migrate to depths of 275 to 400 meters where they remain until the next mating migration (Table 32 and Figures 40 and 41). Some reports conflict with the above observations; therefore, the behavior may vary somewhat. On the basis of tagging experiment results, Kato, et al., (1965) suggested that these crabs migrate into shallow water about November and, after copulation with females, return to deeper water in March. "Conversely, Yoshida (1941), after interviewing a number of fishermen, concluded that during March and April the male population shifts deeper from a depth of 70 to 80 fathoms to 100 fathoms, where they encounter the aggregated mature female crabs" (Pereyra, 1967). Males larger than 90 mm carapace width are present at depths less than 275 meters only temporarily during seasonal migrations (Kon, 1969). Within the Gulf of St. Lawrence the behavior of *C. opilio* seems to be quite similar. Although some crabs travelled 35 miles in less than one year, the average movement of autumn tagged crabs was only 10.9 miles (Watson, 1972; Table 34). It appears that most adult *C. opilio* remain above 100 fathoms in the Gulf of St. Lawrence.

CONCLUSIONS

1. Mature female *Chionoecetes opilio* are quite fecund in respect both to number of eggs produced per individual (5,500 to 150,000) and frequency of berried individuals (Ito, 1967; Powles, 1966; Watson, 1969). Comparative fecundity in successive age groups of multiparous females has not been reported in the literature and awaits further study.

2. *C. opilio* has a relatively long larval life (estimates vary from two months to seven or eight months). The four larval stages (prezoea, zoea I, zoea II, and megalops) are very small (their respective total lengths: 3 mm; 4 to 5 mm; 6 to 7 mm; and 6 to 7 mm) and lead a planktonic existence.

3. Laboratory rearing experiments indicate that temperature and specific gravity are two important factors affecting the success and rate of development of larvae. Optimal temperatures lie in the range of 7.9 to 12.9°C for zoea I, 7.1 to 10.7°C for zoea II, and 12.5 to 17.4°C for megalops. Optimal specific gravities are 1.020 to 1.022 for zoea I, and 1.019 to 1.026 for zoea II. Differences in the temperature tolerances of the two forms of *C. opilio* may be a major limiting factor to their distributions.

4. The amount of time which elapses during the downward migration of megalops has not been determined. However the time involved is a key factor in accurately determining the total length of larval life. Mortality may be high among megalops due to prolonged exposure to predators and fluctuations in food availability before and during the migration to the sea floor. Published data concerning these subjects is lacking.

5. The first instars are found on the sea floor (of the Sea of Japan) at depths of 300 to 400 meters. As they continue to grow, the instars gradually migrate to shallower areas. In the Sea of Japan, instars I to VI are found at depths of 300 to 350 meters, instars VII and VIII are found between 200 and 400 meters, and instars IX and X occur between 200 and 250 meters. Bering Sea juvenile *C. opilio* (23 to 44 mm carapace width) do not migrate beyond the zone of 60 to 80 meters (Tarverdieva, 1976).

6. The growth rate of *C. opilio* decreases during the last several molts before the molt to maturity. Female crabs undergo a terminal molt to maturity. Adult males grow at a decreased (but relatively uniform) rate.

7. The bathymetric distributions (in the Sea of Japan) of mature male
    and mature female crabs overlap but are slightly different. Female
    primary spawners are found at 200 to 250 meters and 275 to 350
    meters, multiparous female crabs are found at 240 to 260 meters, and
    mature males are widespread between 200 and 400 meters although those
    with carapace widths greater than 90 mm are uncommon at depths less
    than 275 meters. Gulf of St. Lawrence *C. opilio* occur between
    approximately 35 and 235 meters with greatest numbers between 90 and
    165 meters (Watson, 1969). Adult *C. opilio* are abundant between
    60 and 130 meters in the southeastern Bering Sea and perform regular
    seasonal migrations (Slizkin, 1974).

8. Adult male crabs probably undergo at least two molts. Tentative
    carapace width modes for adult males are: 77.7 mm (Adult I);
    91.4 mm (Adult II); 111.2 mm (Adult III); and 132.4 mm (Adult IV).
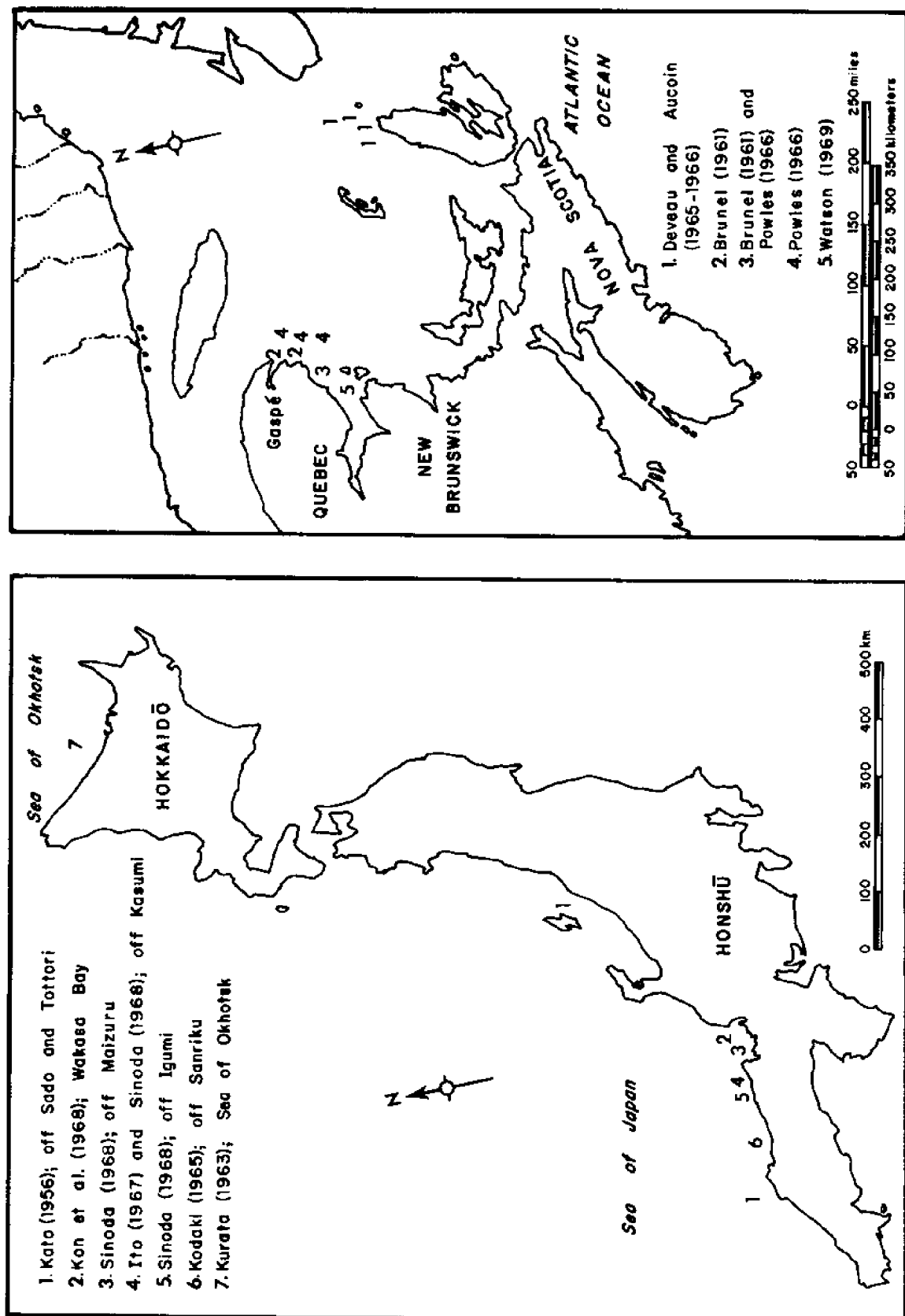
Figure 1. Location of several important study areas off Japan and eastern Canada

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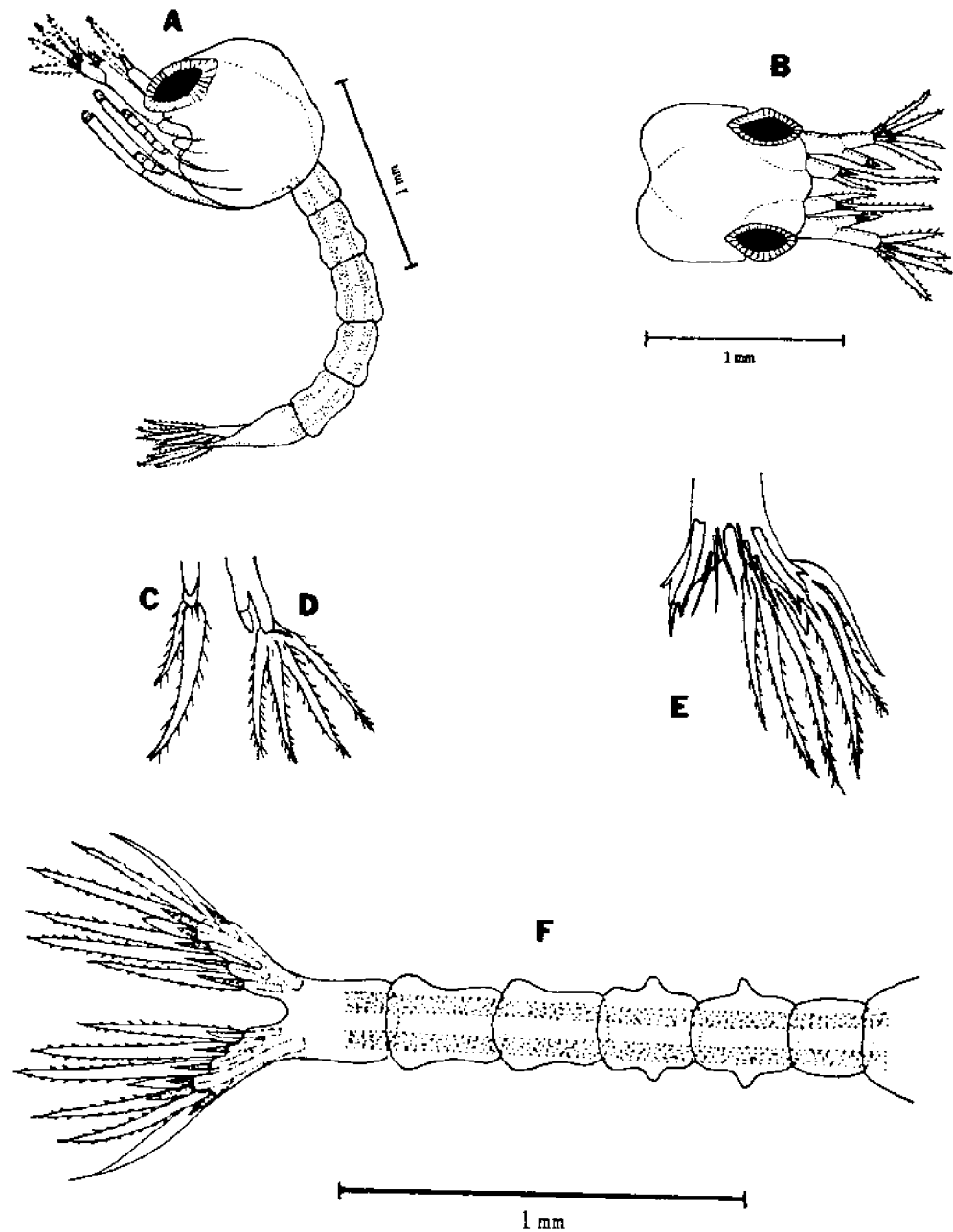
Figure 2. *Chionoecetes opilio* prezoea. A. Lateral view (from Kuwatani et al., 1971) B. Anterior view (from Kuwatani et al., 1971) C. First antenna (from Kon, 1967) D. Second antenna (from Kon, 1967) E. Telson (from Kon, 1967) F. Abdomen and telson (from Kuwatani et al., 1973)
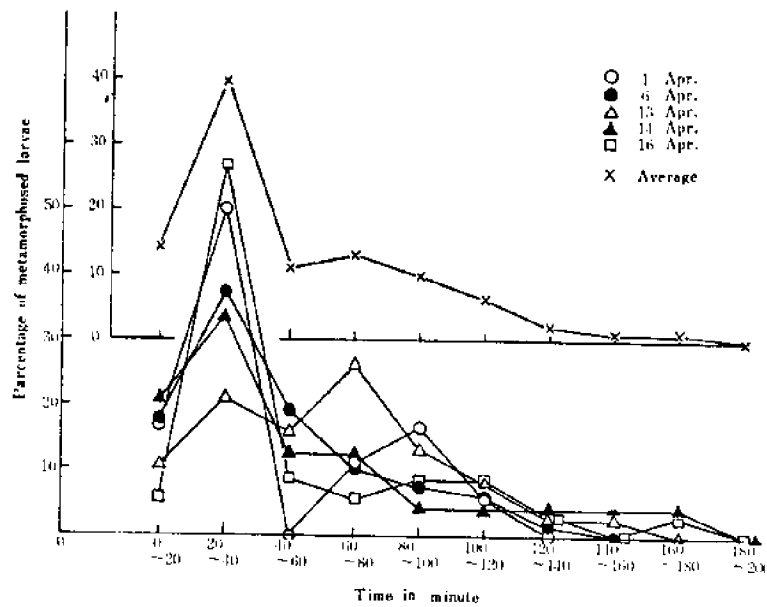
Figure 3.   Time required for metamorphosis from hatching to the first
            stage zoea (from Kuwatani et al., 1971)

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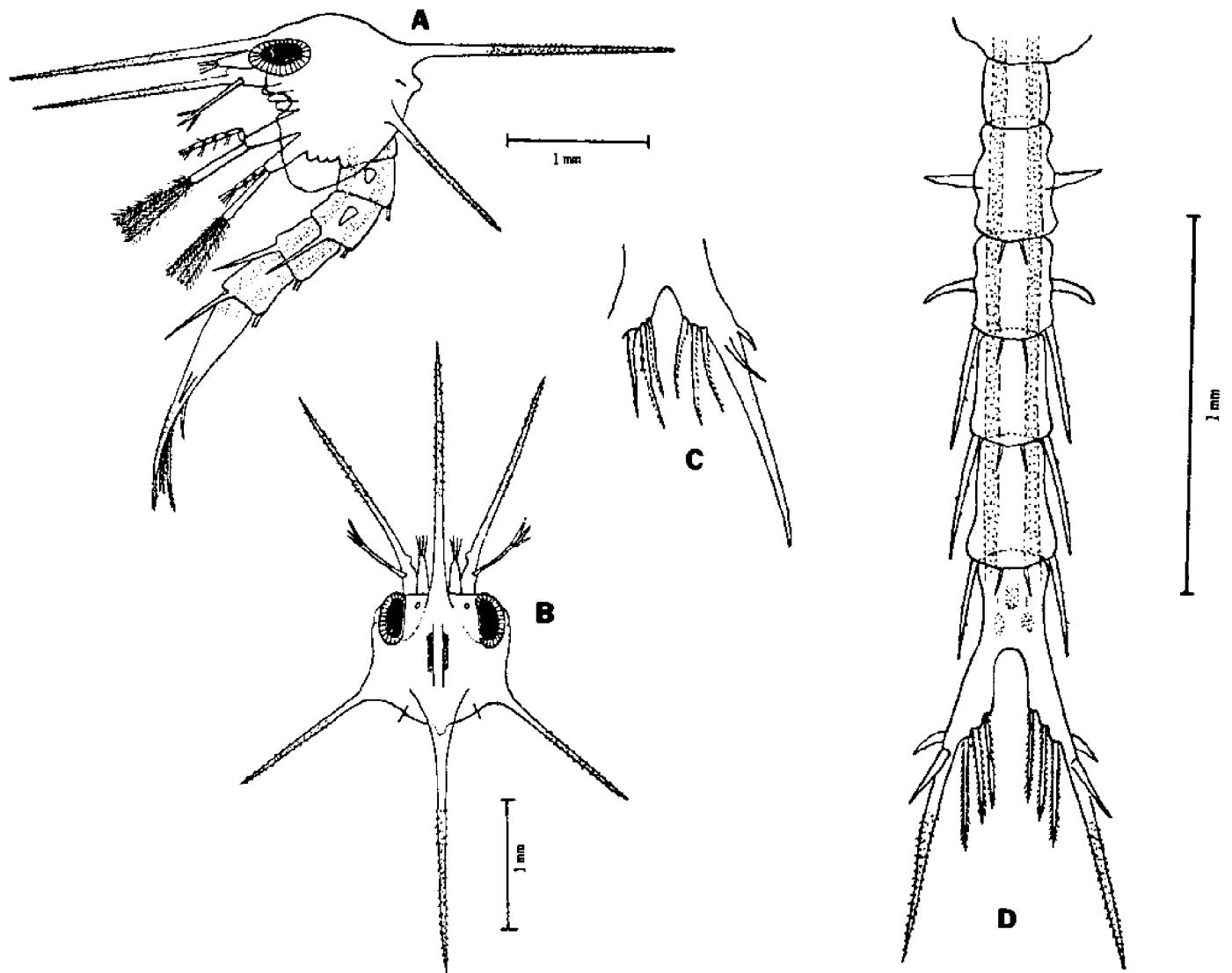
Figure 4.   *Chionoecetes opilio* zoea.   A.   Lateral view (from Kuwatani et al., 1971)   B.   Anterior view (from Kuwatani et al., 1971)   C.   Telson (from Kon, 1967)   D.   Abdomen and telson (from Kuwatani et al., 1971)
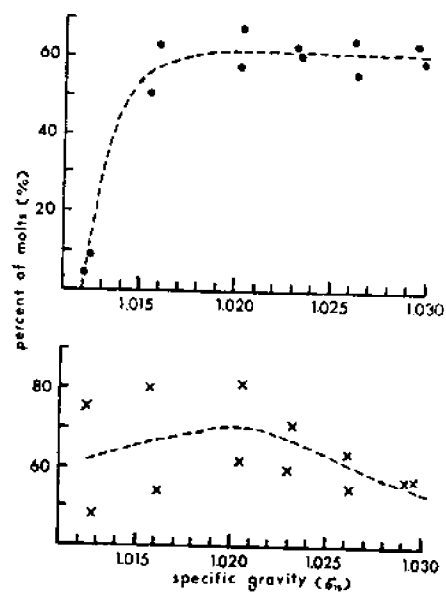
Figure 5a. Comparison of the integral temperature required for the first
zoeal molt between the newly hatched larvae of *Chionoecetes
opilio* transferred directly and those transferred gradually
from hatching sea water to rearing sea water (varying specific
gravity). .––direct transfer, x––gradual transfer (from Kon, 1973)

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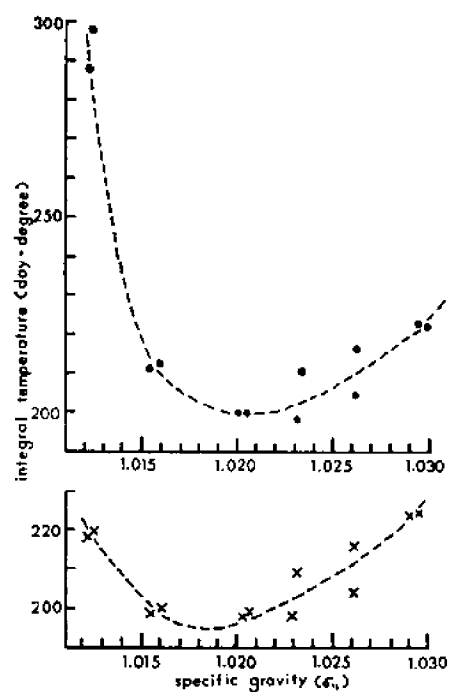
Figure 5b. Comparison between the percentage of molts obtained from the first zoeal molt of the newly hatched larvae of *Chionoecetes opilio* transferred directly and transferred gradually from hatching sea water to rearing sea water (varying specific gravity). .—direct transfer, x—gradual transfer (from Kon, 1973)
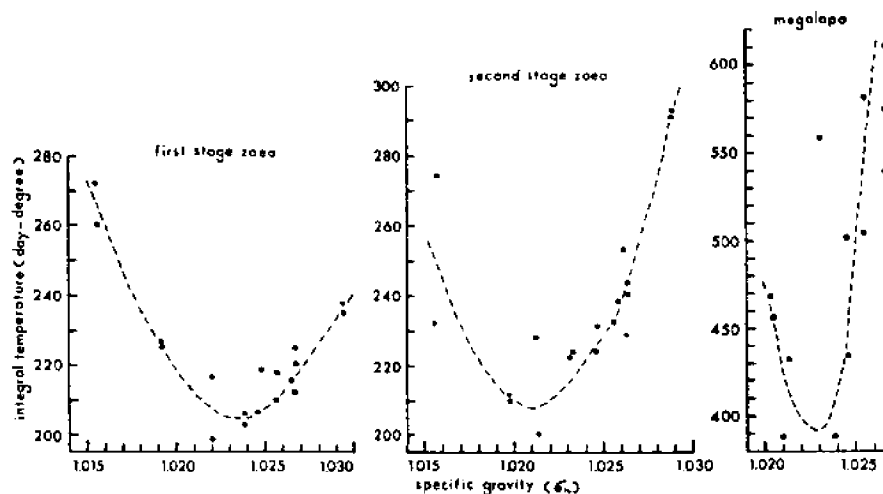
Figure 6a. Effect of specific gravity on the integral
            temperature of each planktonic larval stage
            of *Chionocetes opilio* (from Kon, 1973)

Figure 6b. Effect of specific gravity on the per-
            centage of molts of each planktonic larval
            stage of *Chionoecetes opilio* (from Kon, 1973)

25
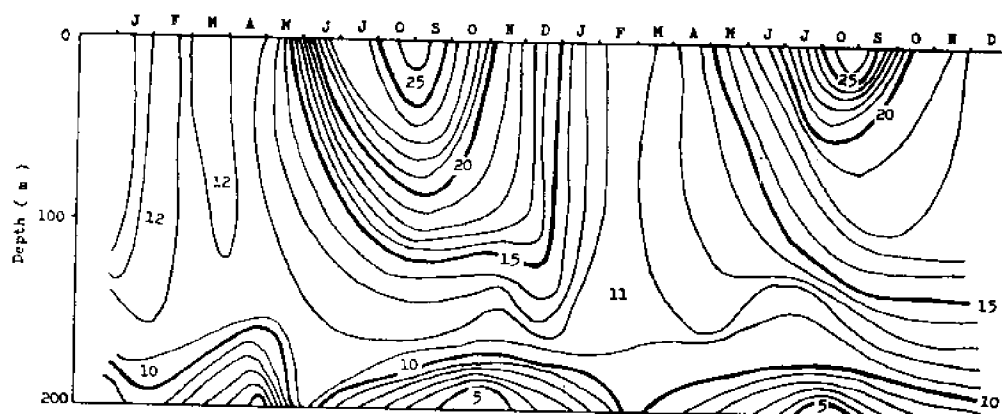
Figure 7.   Seasonal variation of thermal distribution in depth at a station
(36° 00'N, 135° 50'E, 260 m deep) off Wakasa Bay in the Sea of
Japan (from Kon, 1970)
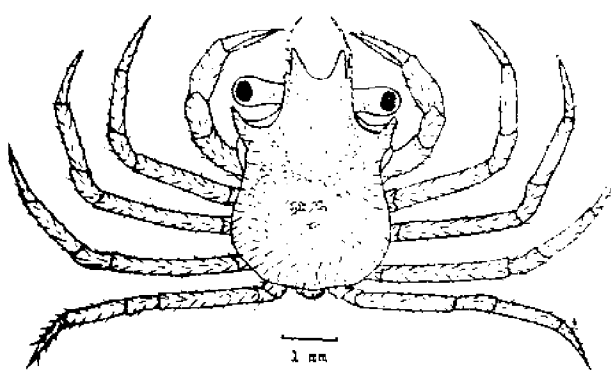
Figure 8. Dorsal view of the first young of snow
          crab (*Chionoecetes opilio*) (from Kon, 1970)
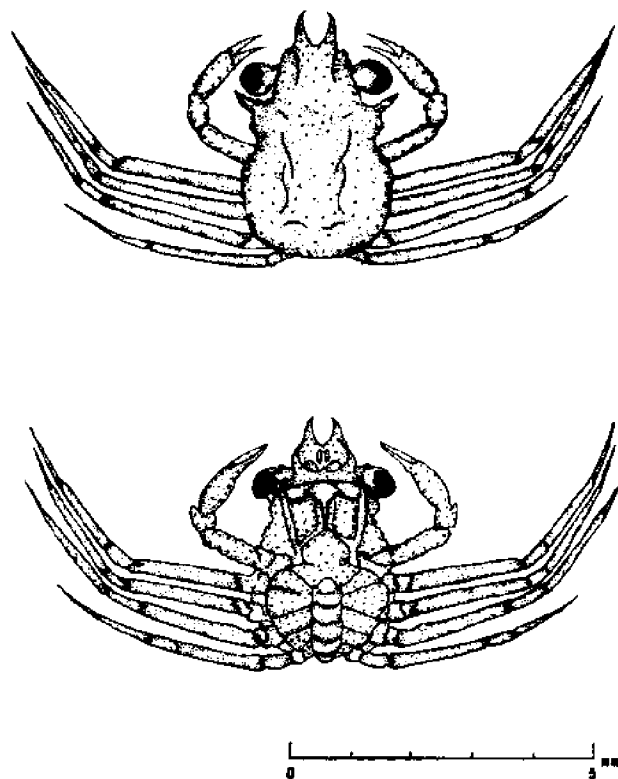
Figure 9. Morphology of the dorsal and abdominal views of *C. opilio* in the first instar stage (from Ito, 1968). Note: Kon (1970) observed that this diagram differs from his own (Figure 8) in the following respects: "...the former has no setae over the whole of its body and its second antennae are extremely short. It looks as though the differences are due to the fact that Ito's specimens had been collected from the stomachs of fish."

$$L_t = 180.4 \ (1 - e^{-0.165(t - 7.267)})$$
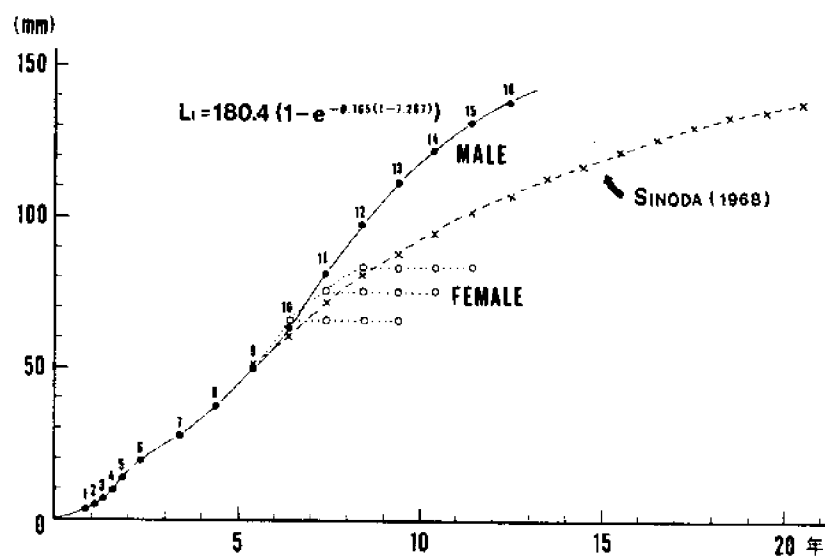
Figure 10. The relationship between growth in carapace width and age (from Ito, 1970)

29
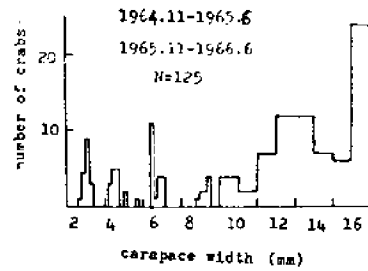
Figure 11a. Frequency distribution of the carapace width in immature *Chionoecetes opilio* smaller than 18 mm width (from Kon et al., 1968)
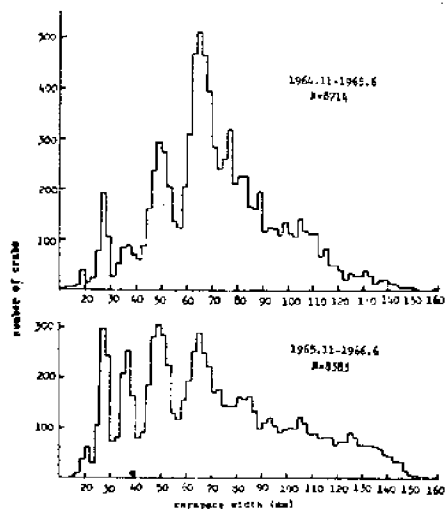
Figure 11b. Frequency distribution of the carapace width in male crabs larger than 10 mm width (from Kon et al., 1968)
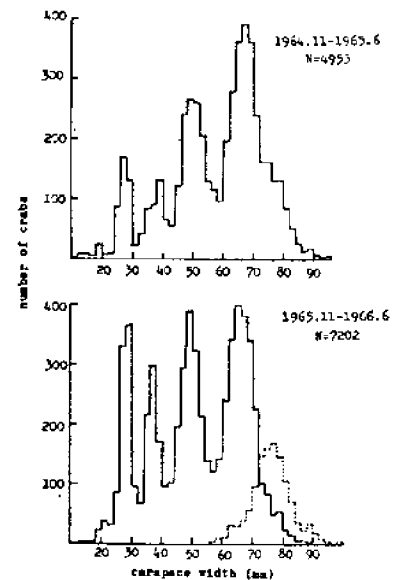
Figure 11c. Frequency distribution of the carapace width in female crabs larger than 10 mm width. Solid line: immature; dotted line: adult (from Kon et al., 1968)

Figure 12. Carapace width frequency of juvenile *C. opilio* (from Watson, 1969)
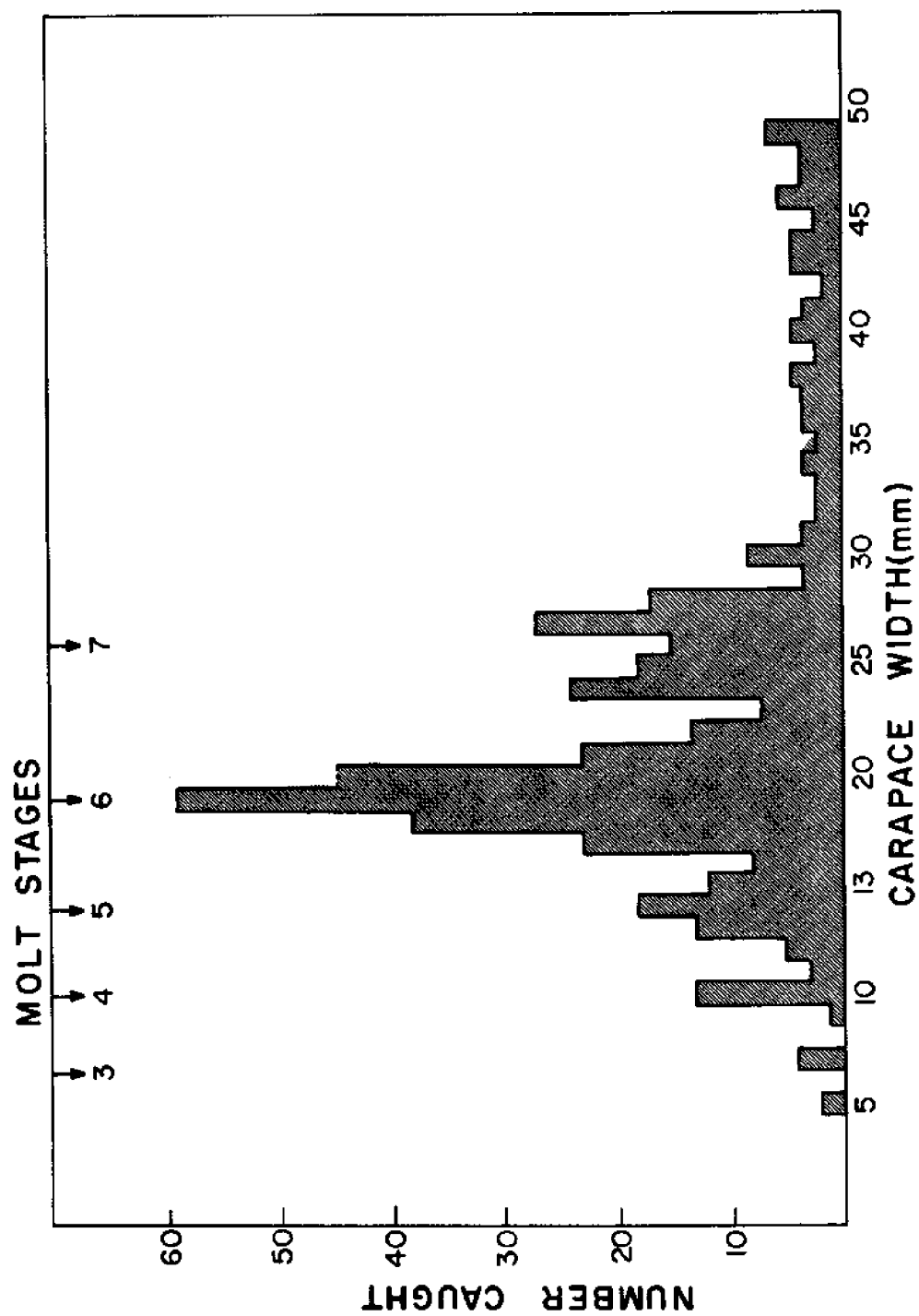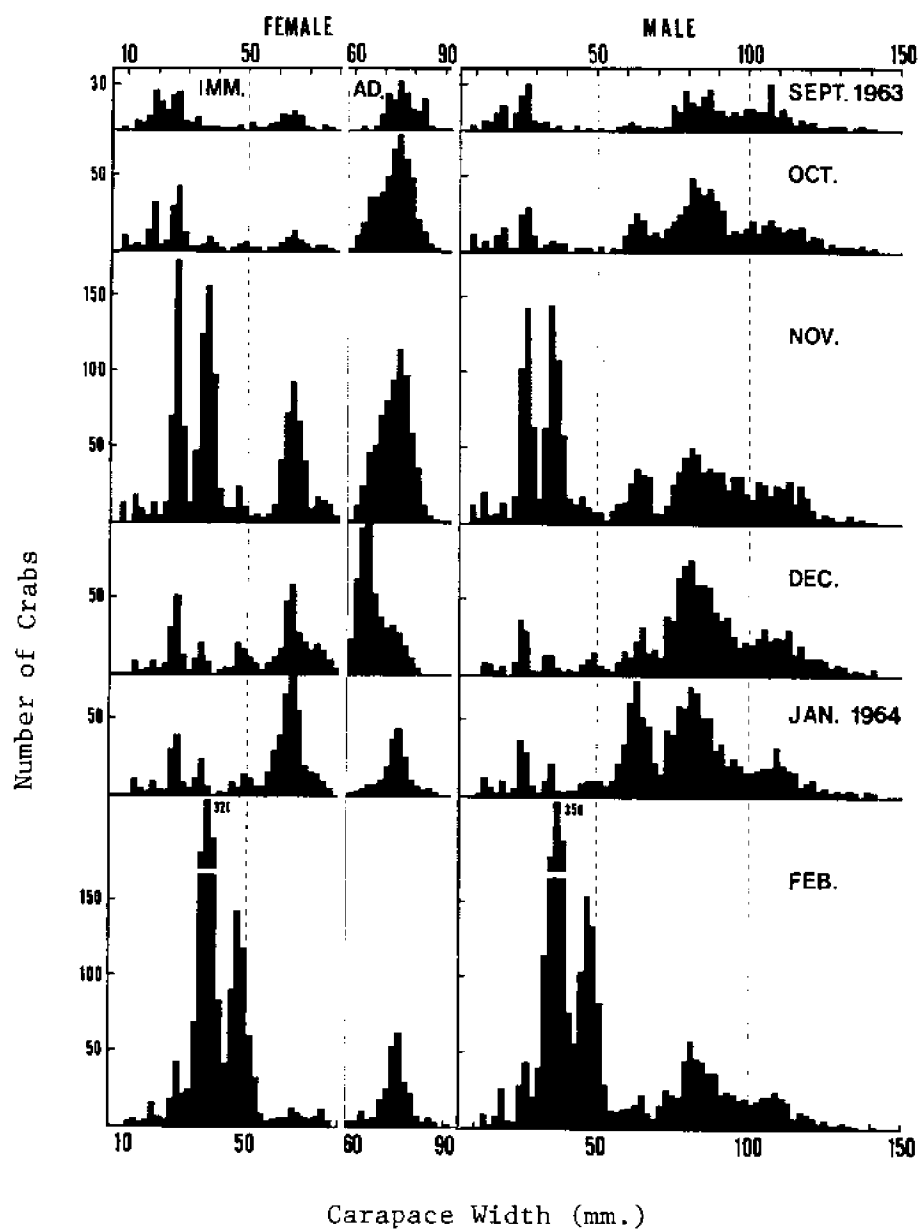
Figure 13. Carapace width frequency of males and females
by months (from Ito, 1970)
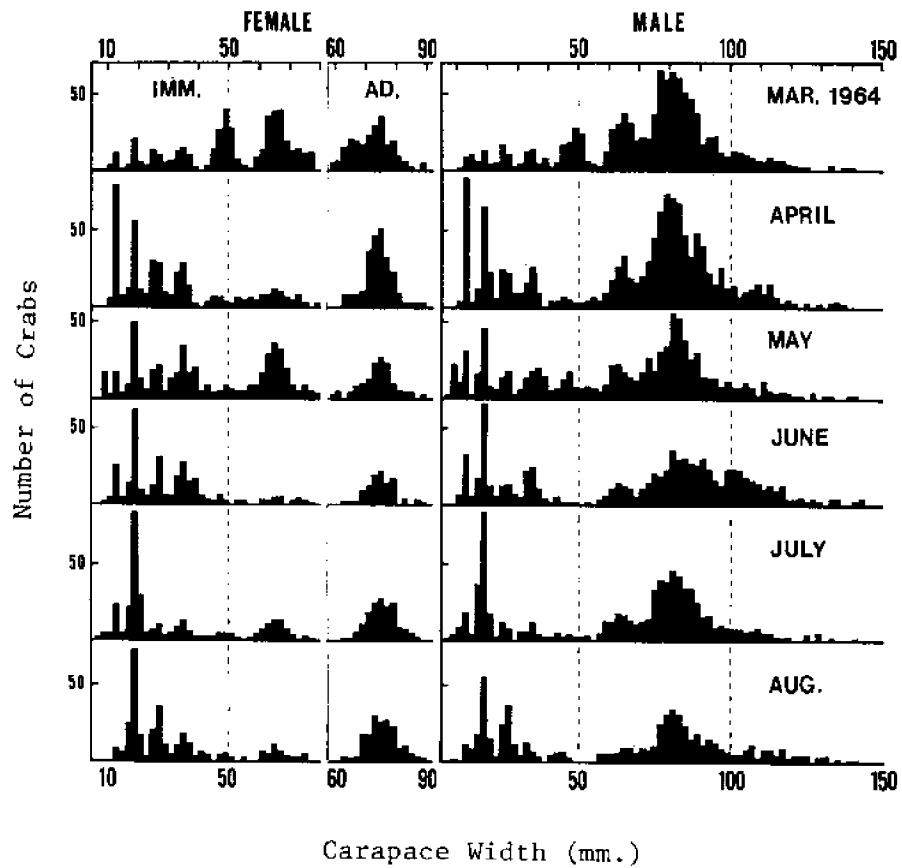
Figure 14. Carapace width frequency of males and females by months (from Ito, 1970)
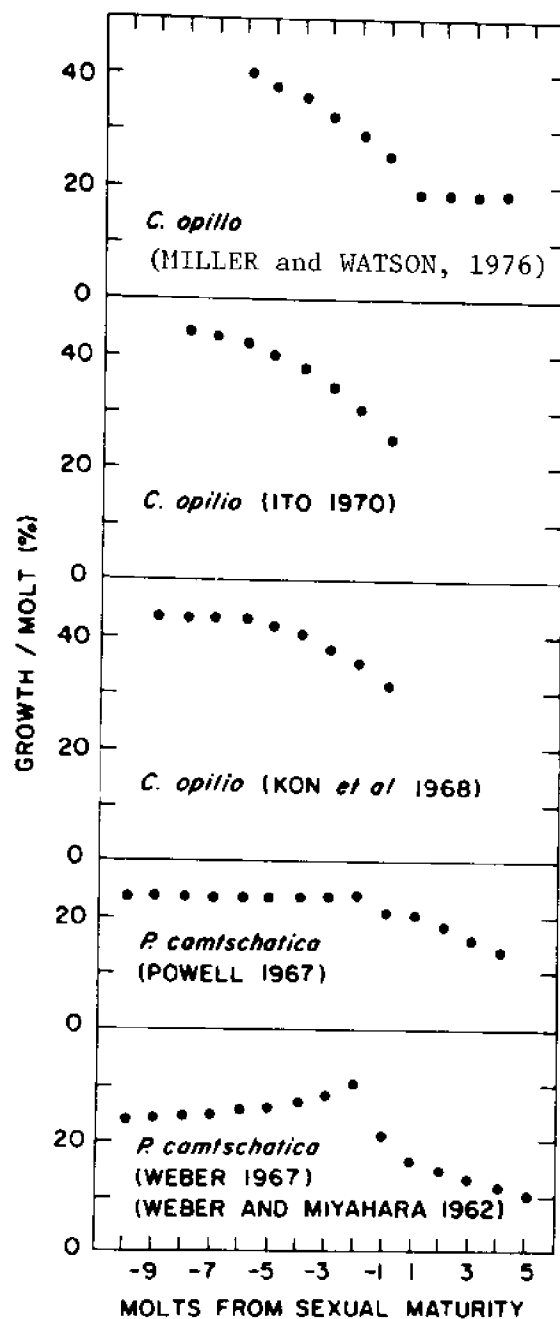
Figure 15. Percentage growth per molt for *C. opilio*
and *Paralithodes camtschatica* with molts
numbered from size at sexual maturity
(from Miller and Watson, 1976)
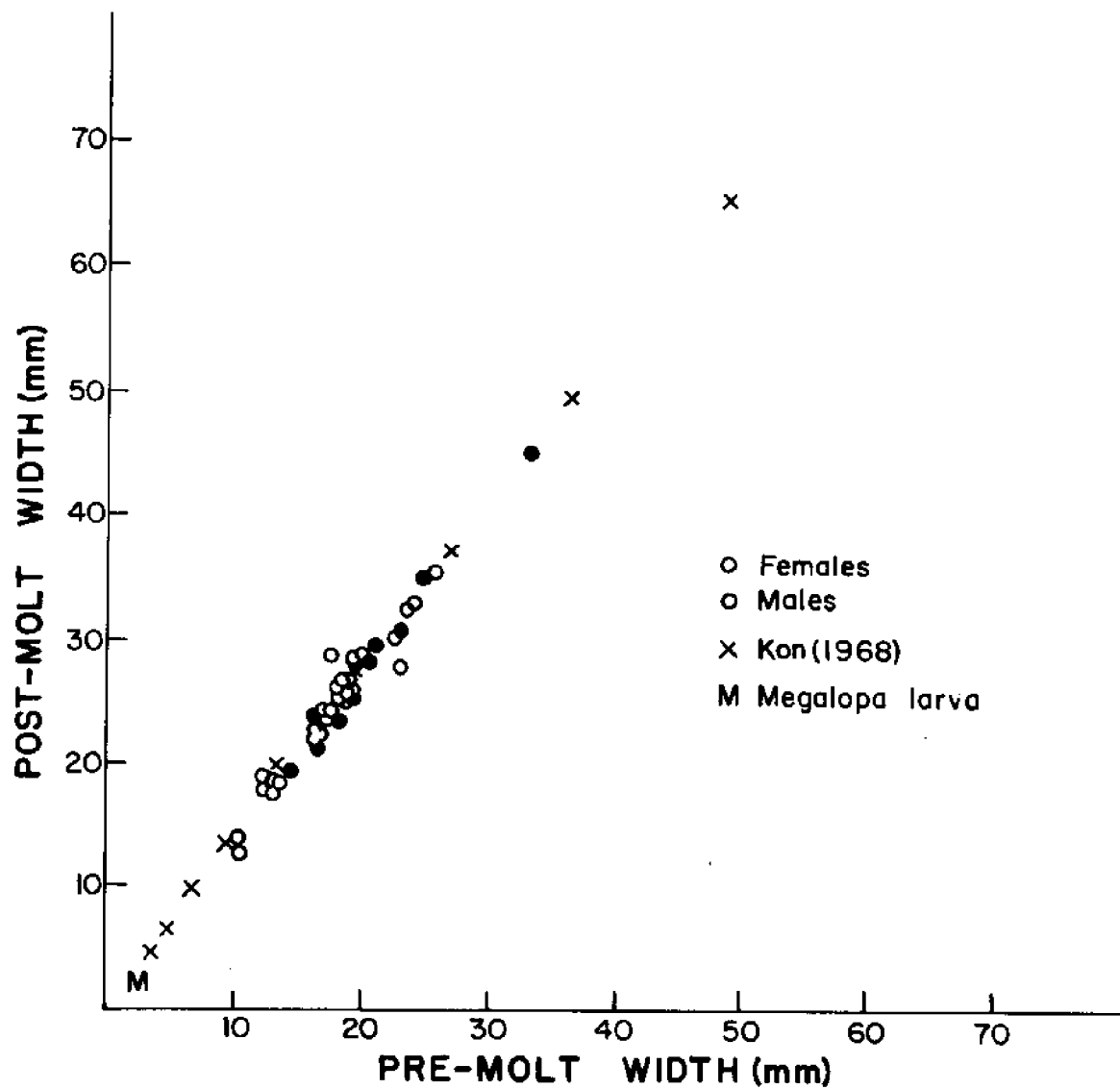
Figure 16. Growth of *C. opilio* (from Watson, 1969)
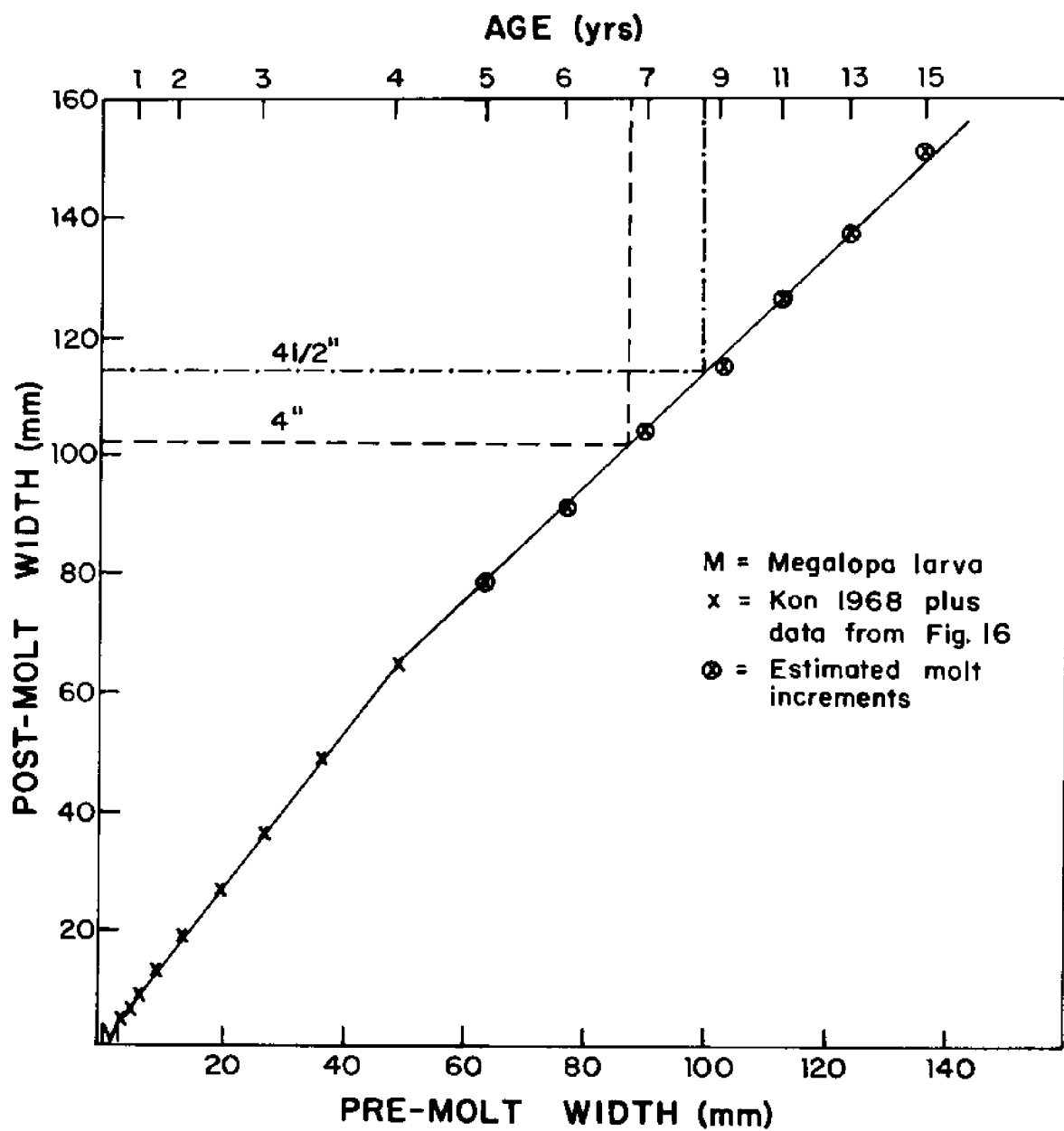
Figure 17.   Preliminary working model for growth and age of
             C. opilio (from Watson, 1969)
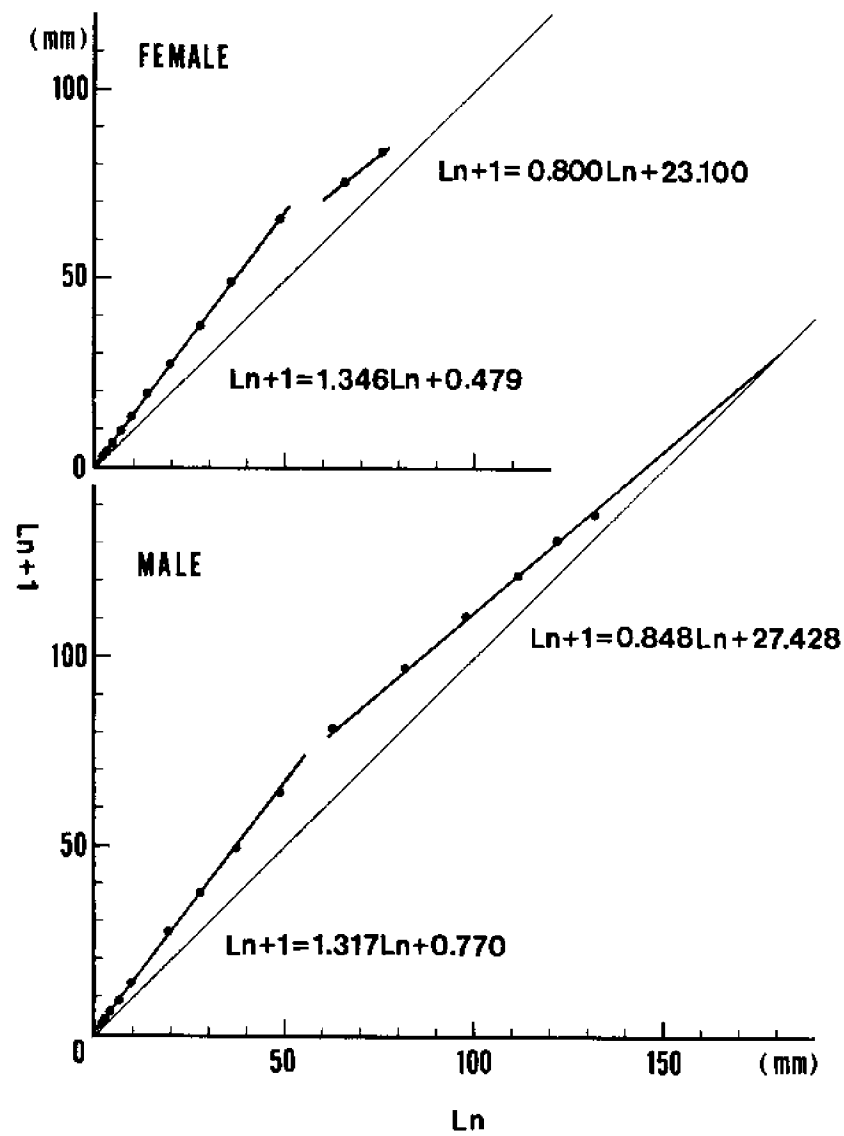
Figure 18. The growth of *C. opilio* illustrated in the graphical technique of Hiatt, 1948 (from Ito, 1970)
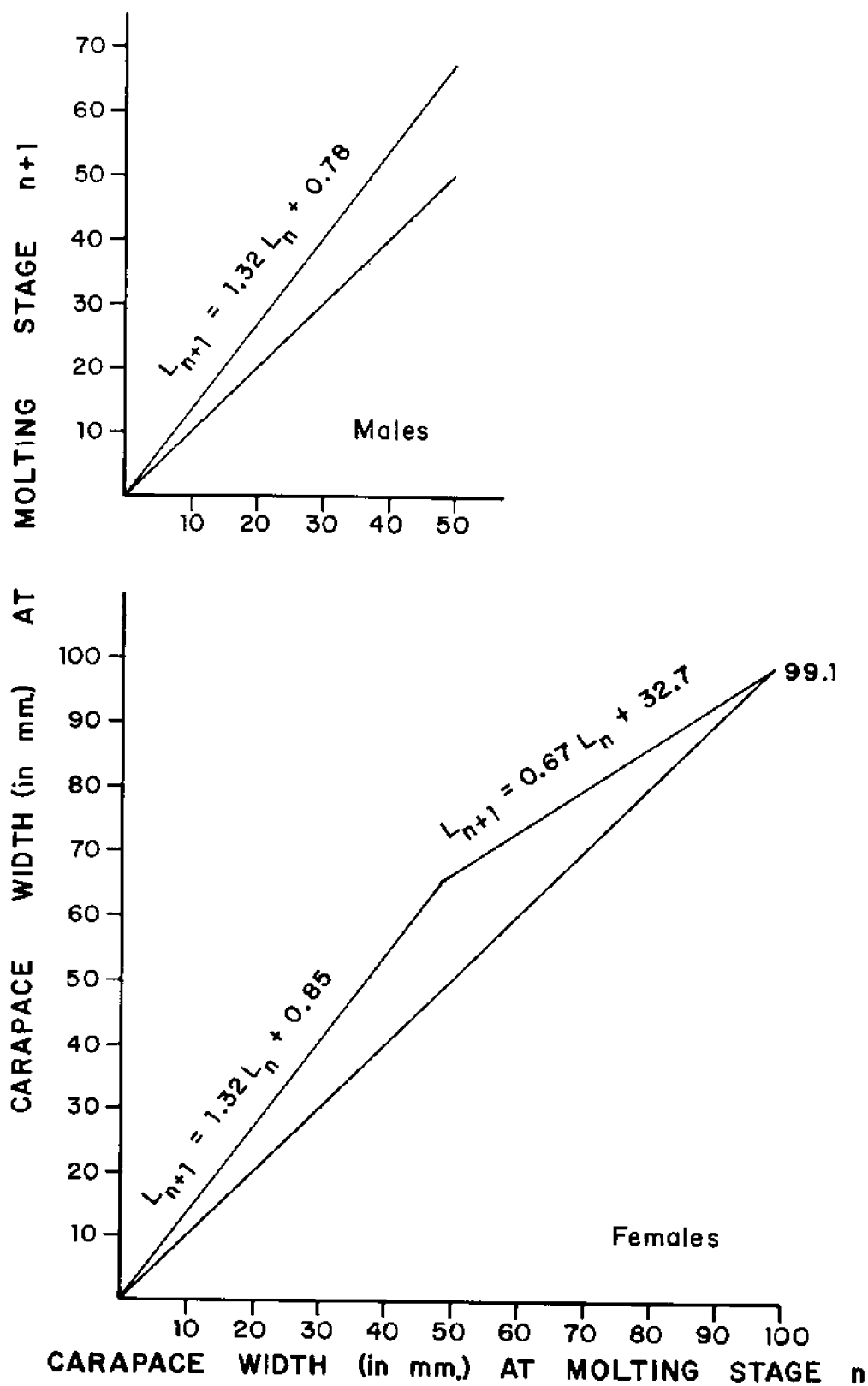
Figure 19. An application of Hiatt's growth diagram to
Chionoecetes opilio (redrawn from Kon et al.,
1968)
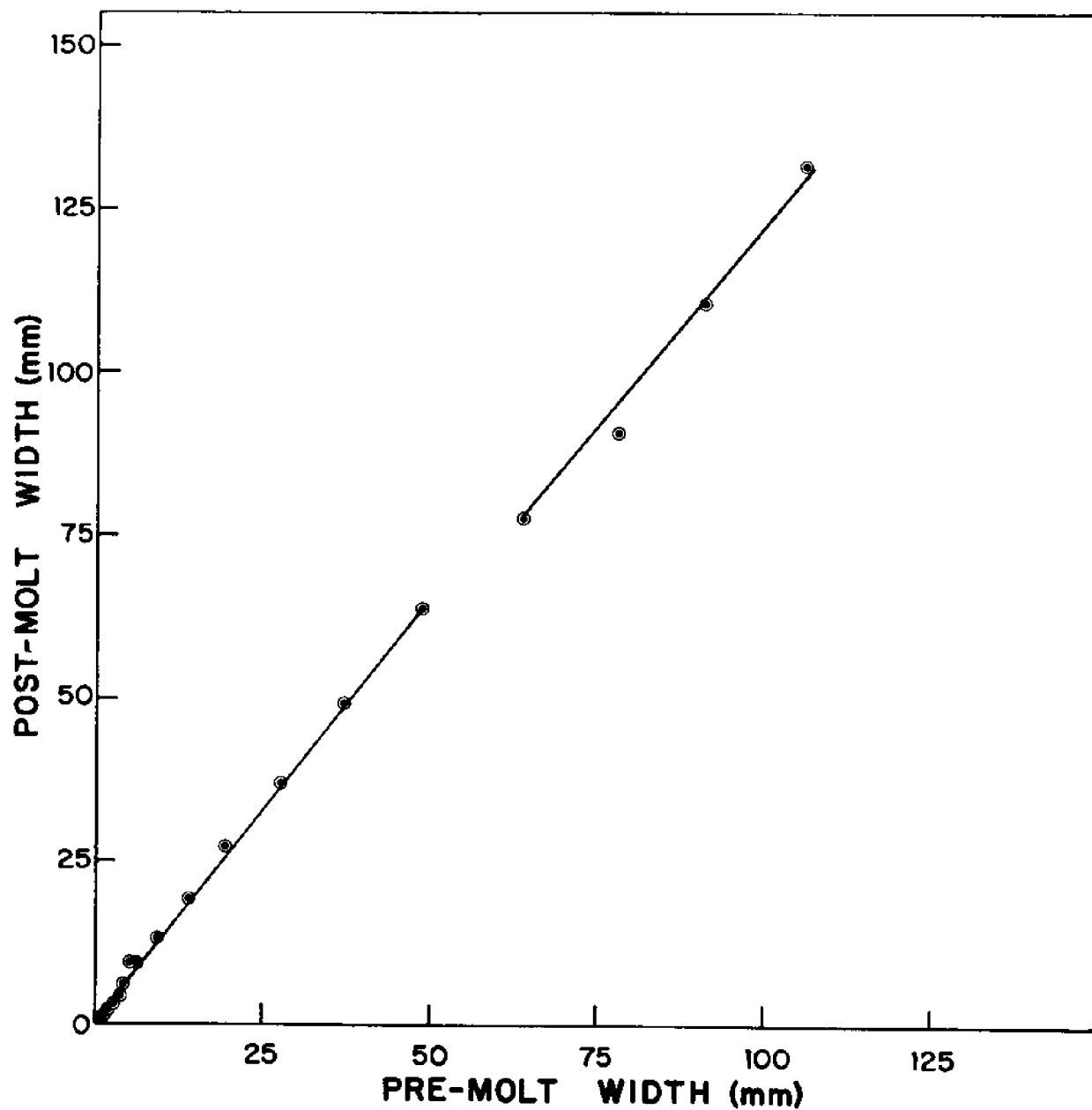
Figure 20. Relationship of post-molt carapace width to pre-molt
carapace width. Values from the growth model for males
(Tables 14 and 15) were used in this figure.
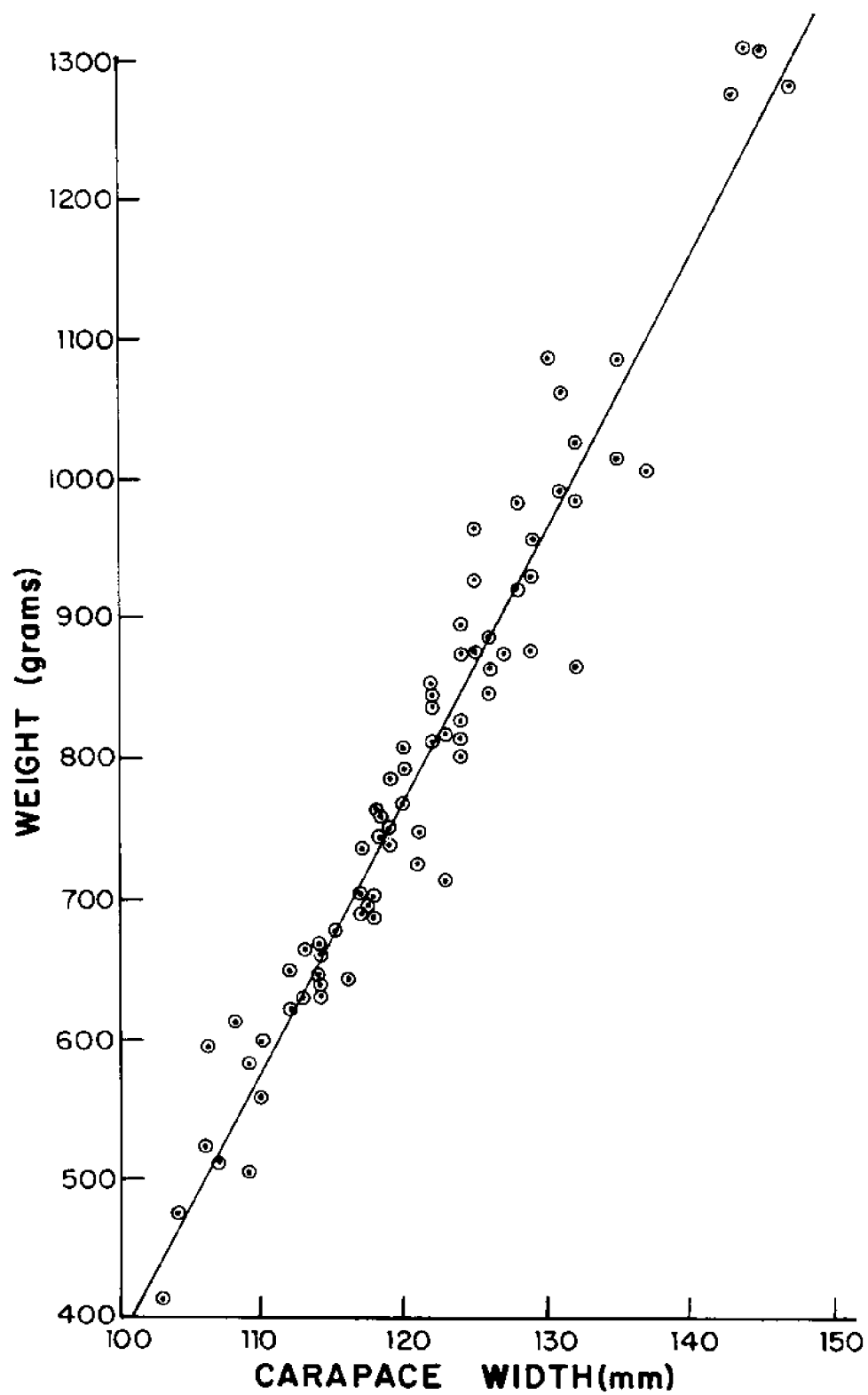
Figure 21. Relationship between carapace width and weight in *Chionoecetes opilio* (from Powles, 1966)
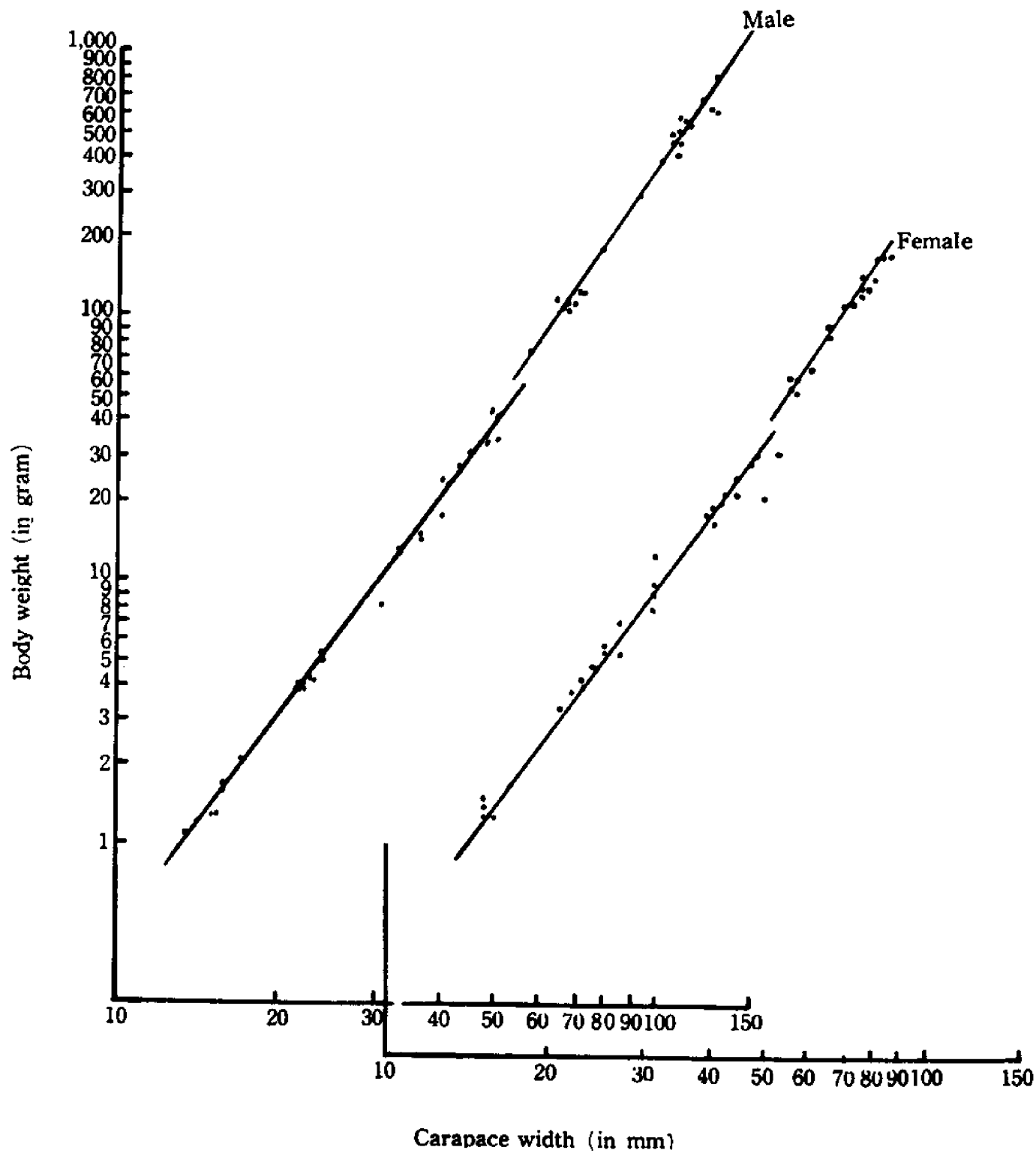
Figure 22. Relationship between the body weight and carapace
width in *Chionoecetes opilio* (from Kanno, 1972)
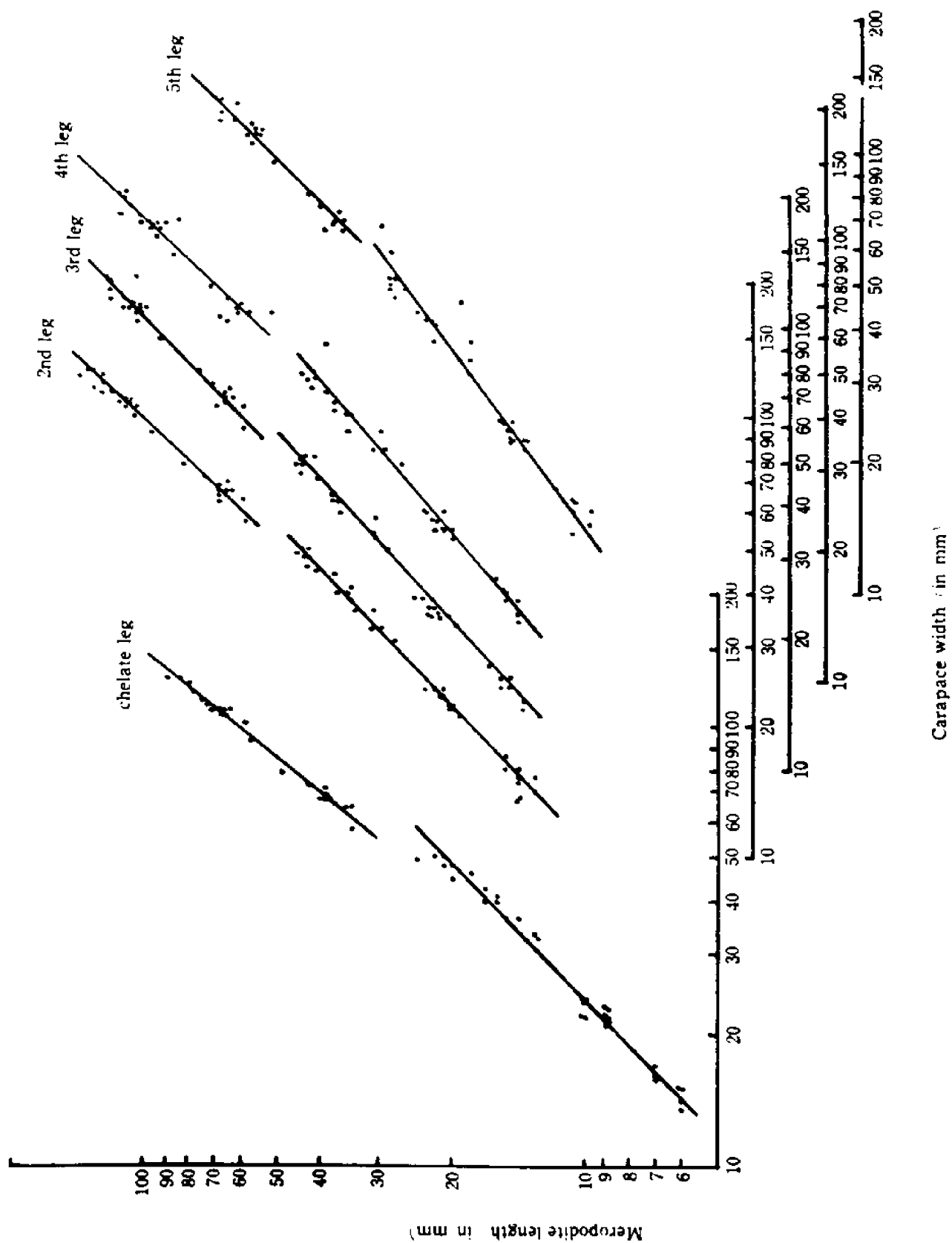
Figure 23a. Relative growth of five meropodites to carapace width in males (from Kanno, 1972)

5th leg

4th leg

3rd leg

2nd leg

chelate leg

Meropodite length in mm)

Carapace width in mm)

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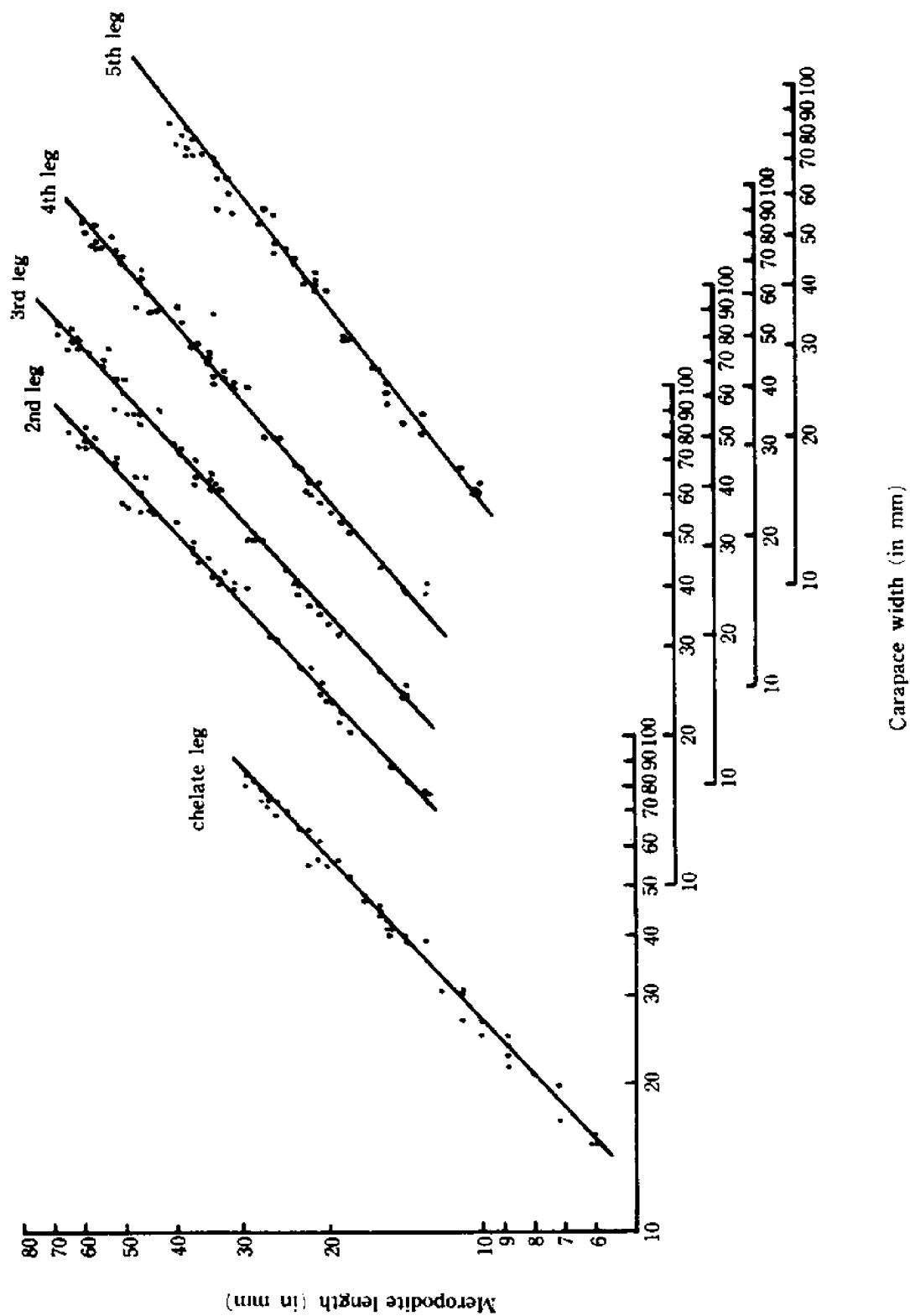
Figure 23b. Relative growth of five meropodites to carapace width in females (from Kanno, 1972)
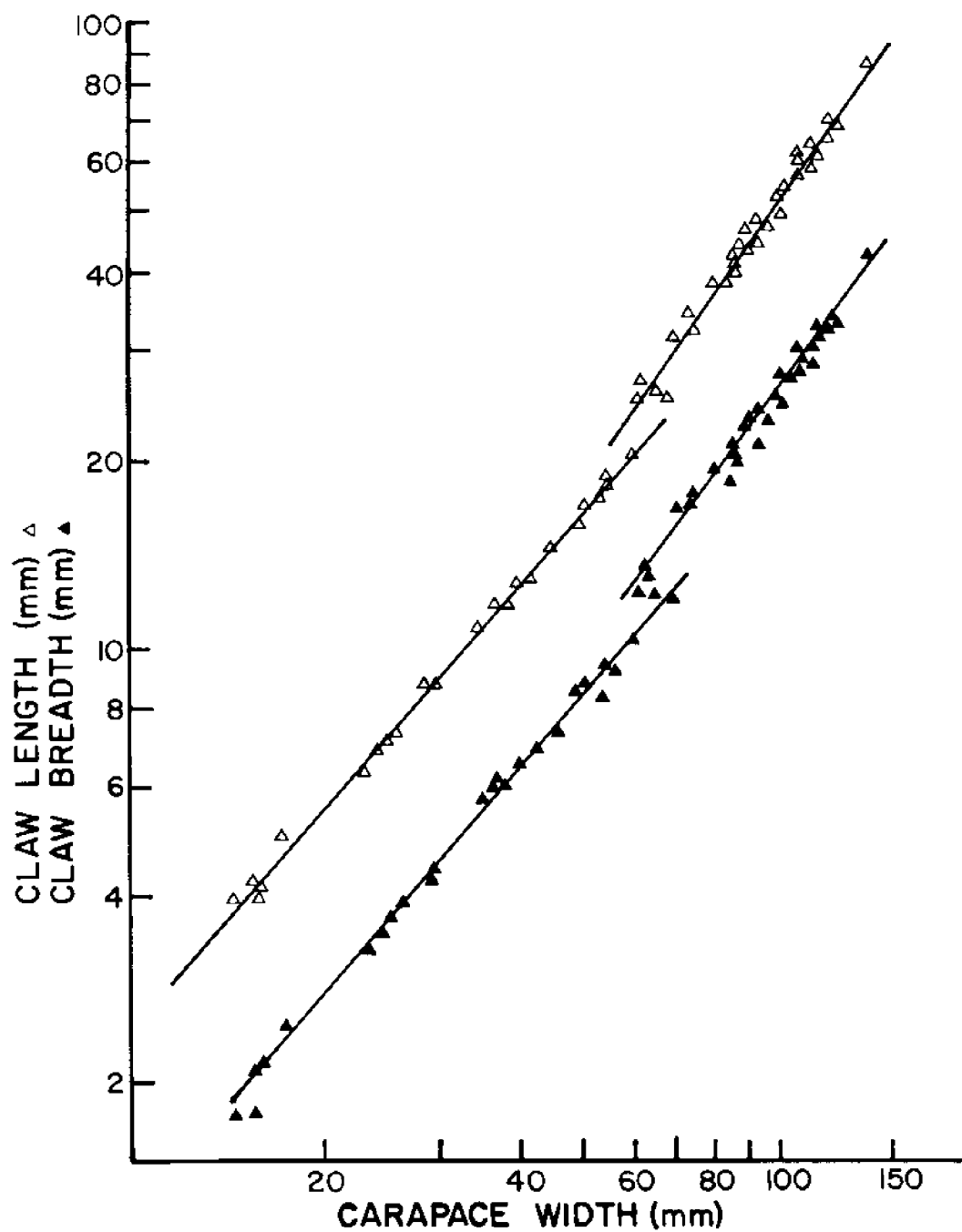
Figure 24. Relationships between claw length and breadth with
carapace width in male *C. opilio* (from Watson, 1969)
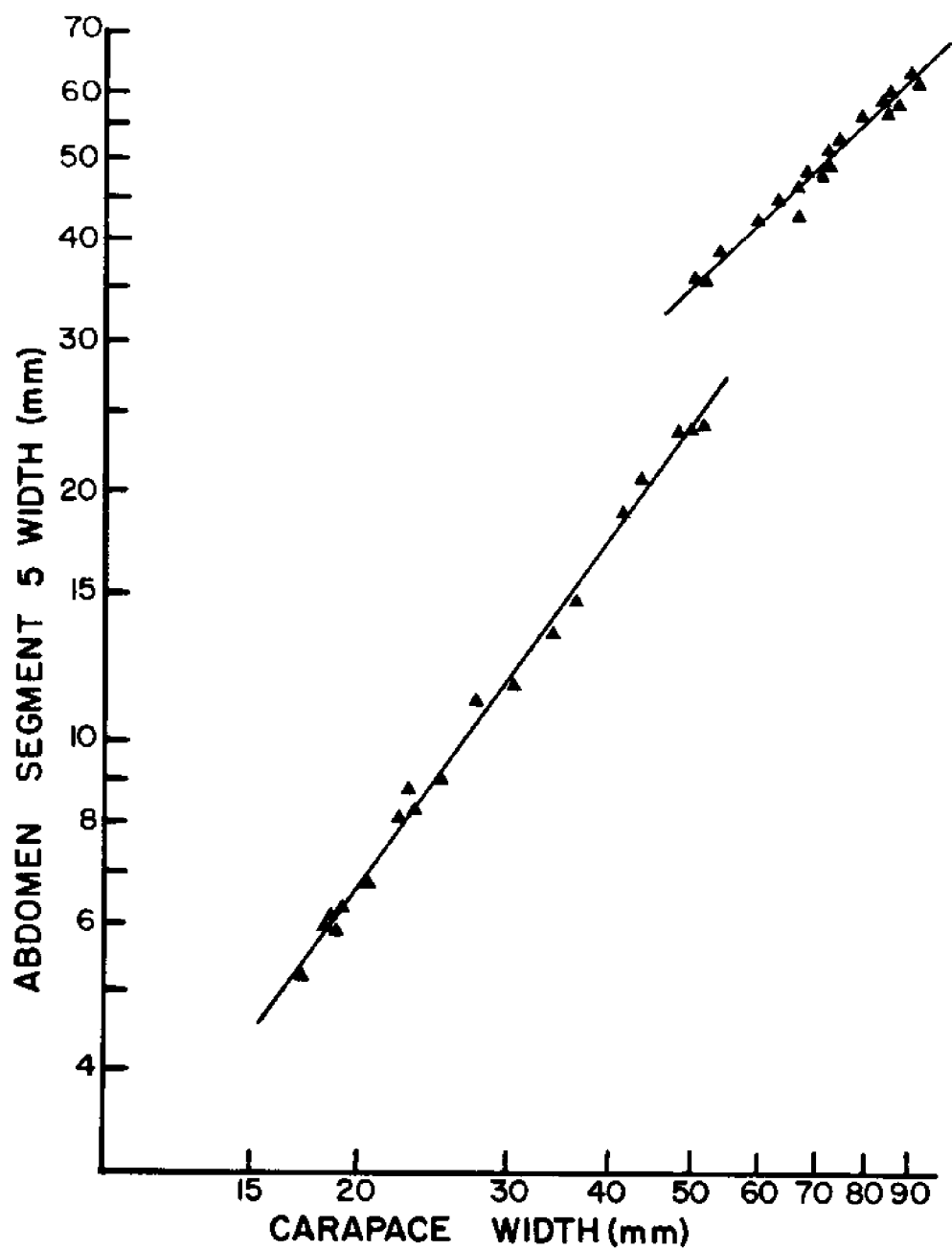
Figure 25. Relationship between carapace width and width of fifth abdominal segment in female *C. opilio* (from Watson, 1969)
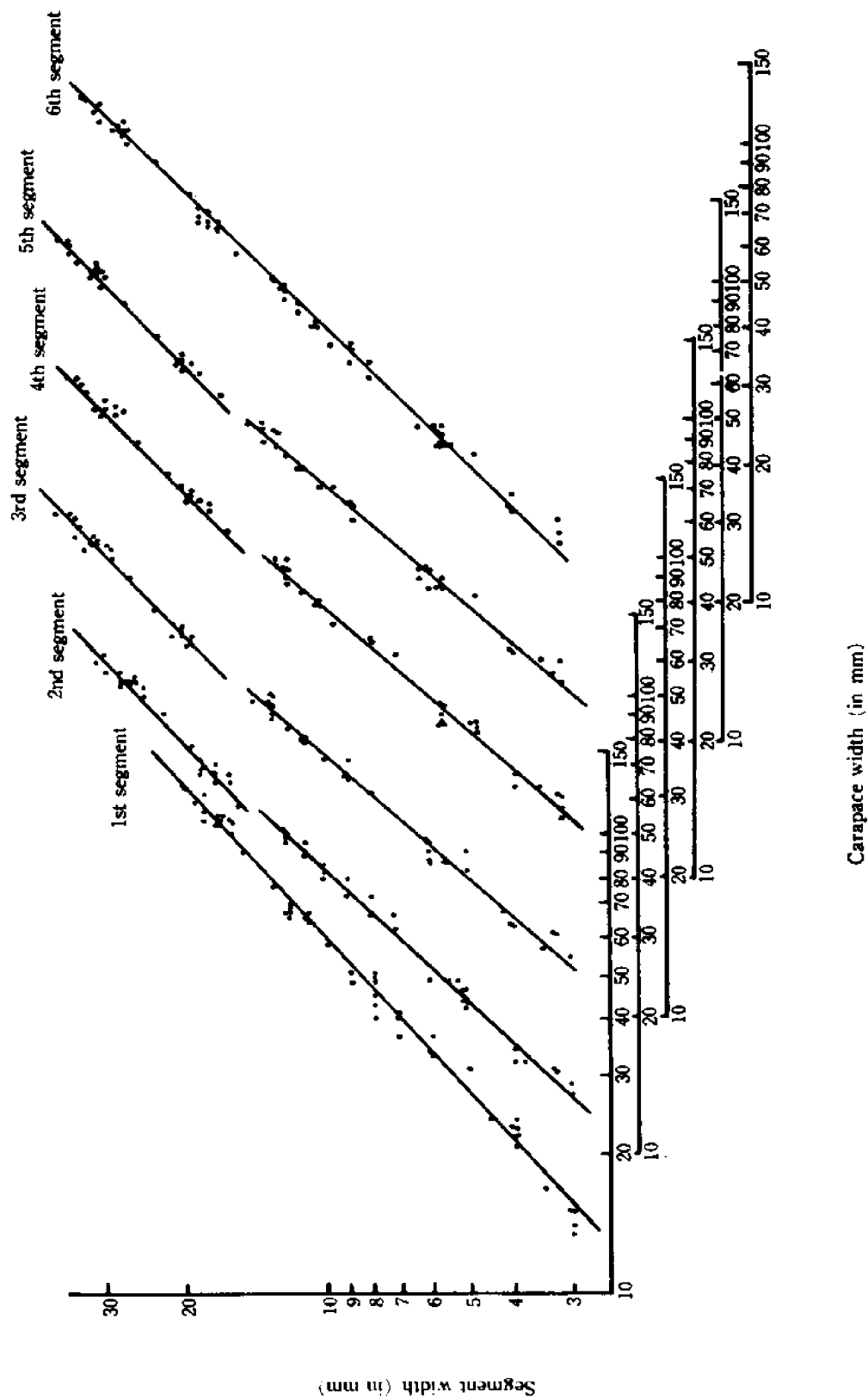
Figure 26a. Relative growth of six abdominal segments to the carapace width in males (from Kanno, 1972)
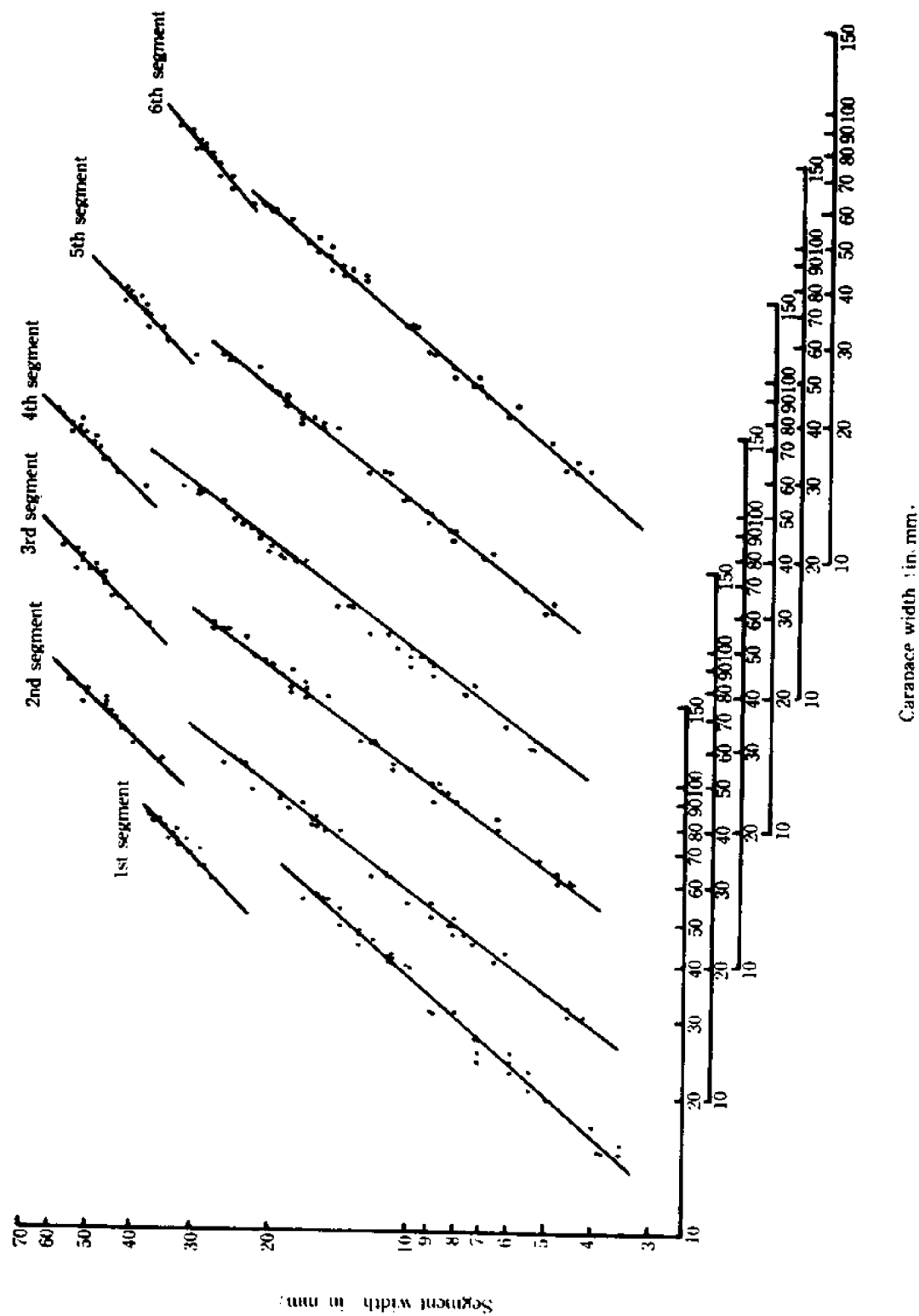
Figure 26b. Relative growth of six abdominal segments to the carapace width in females (from Kanno, 1972)
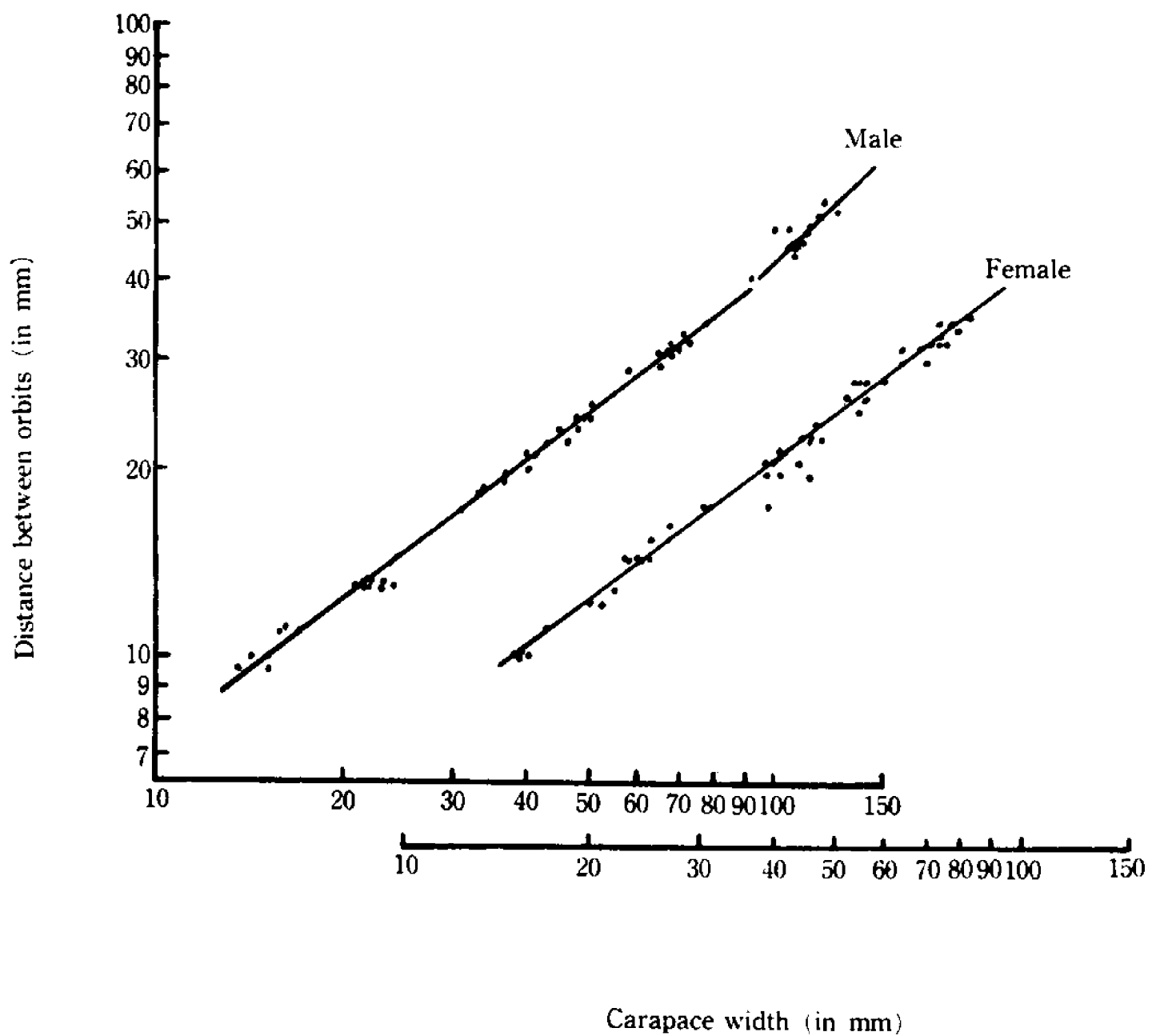
Figure 27. Relative growth of the distance between outer ridges of both orbits to carapace width (from Kanno, 1972)
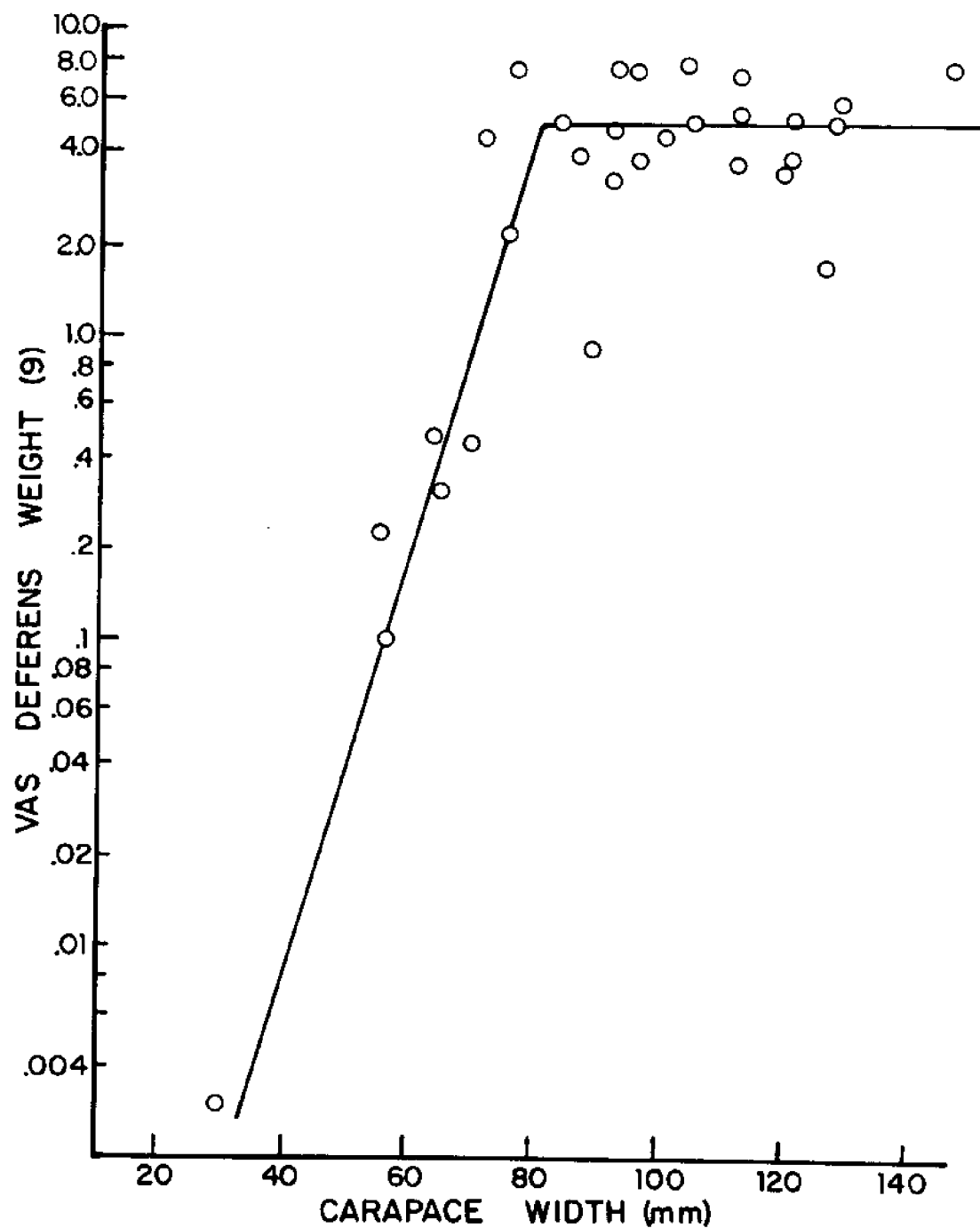
Figure 28. Relationship between weight of vas deferens and
carapace width in male *C. opilio* (from Watson, 1969)
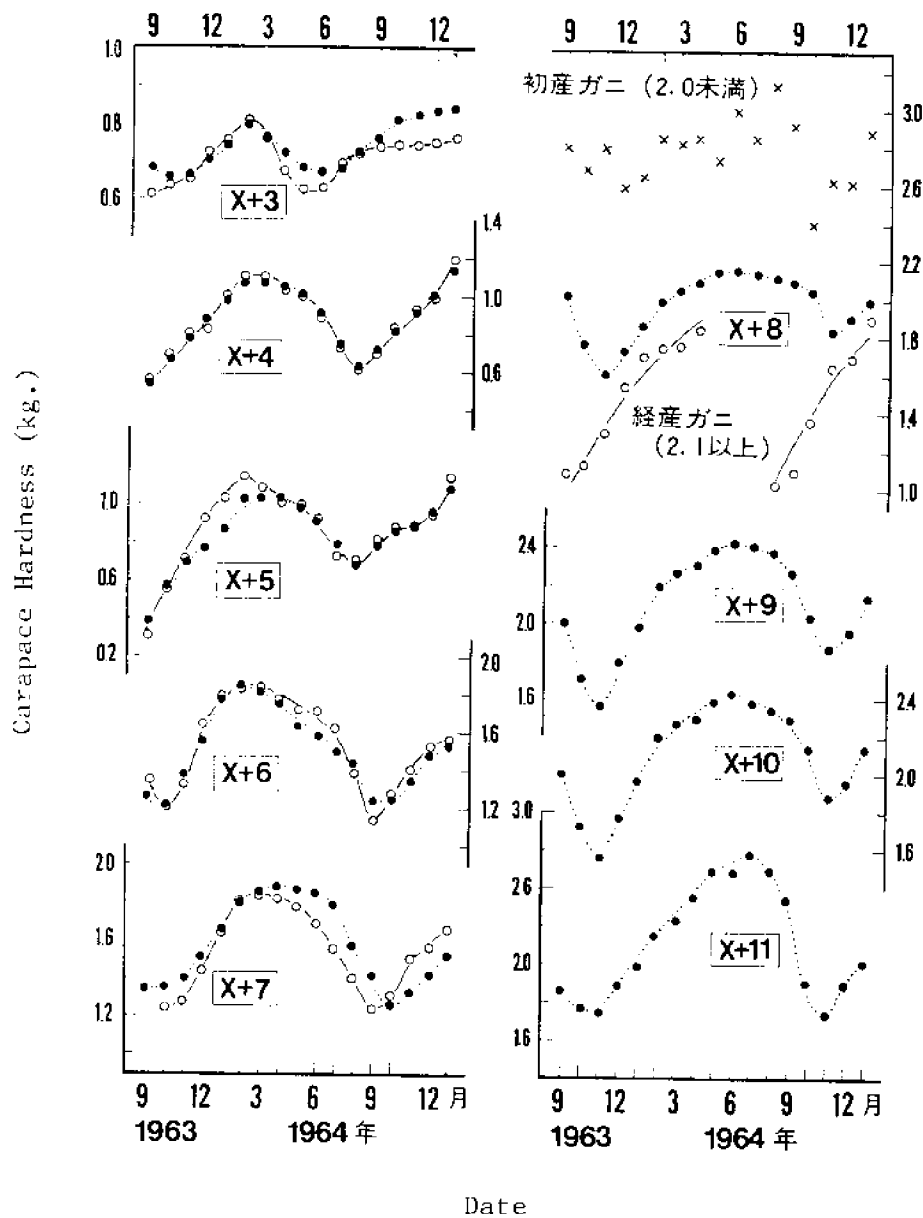
Figure 29. Seasonal variations in the monthly average carapace hardness
by molting stage and sex (from Ito, 1970). Molting stages
are indicated by X + N where X = 3. Values are as follows:
o -- females; . -- males. In the X + 8 molting stage X
values are for multiparous females with carapace hardness
<2.0 and o values are for primiparous females with carapace
hardness >2.1

Figure 30. Seasonal variation in the rate of occurrence of soft-carapaced crabs and double-carapaced crabs by molting stage and sex (from Ito, 1970)
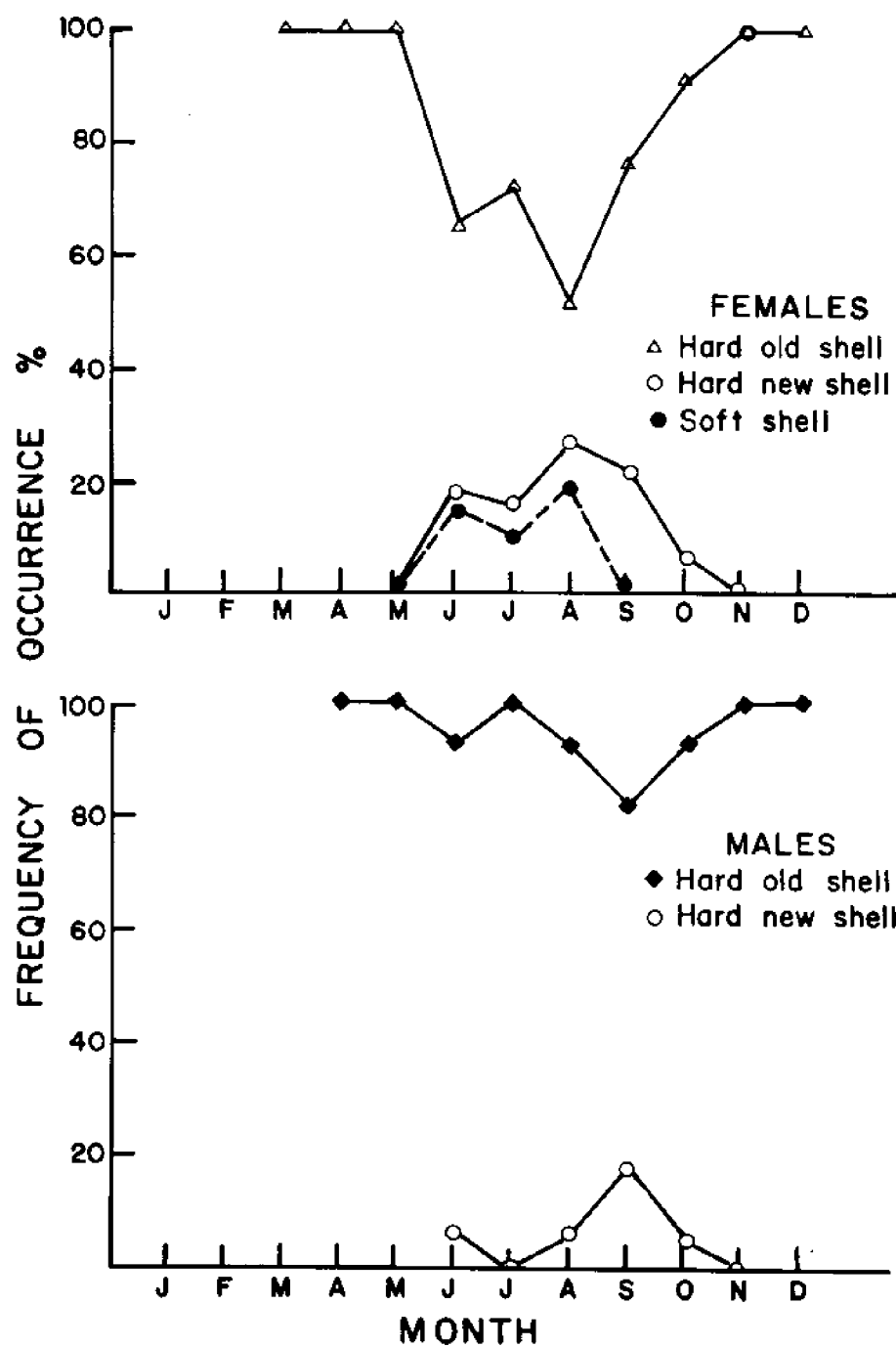
Figure 31. Seasonal shell condition of male and female *C. opilio* (from Watson, 1969)
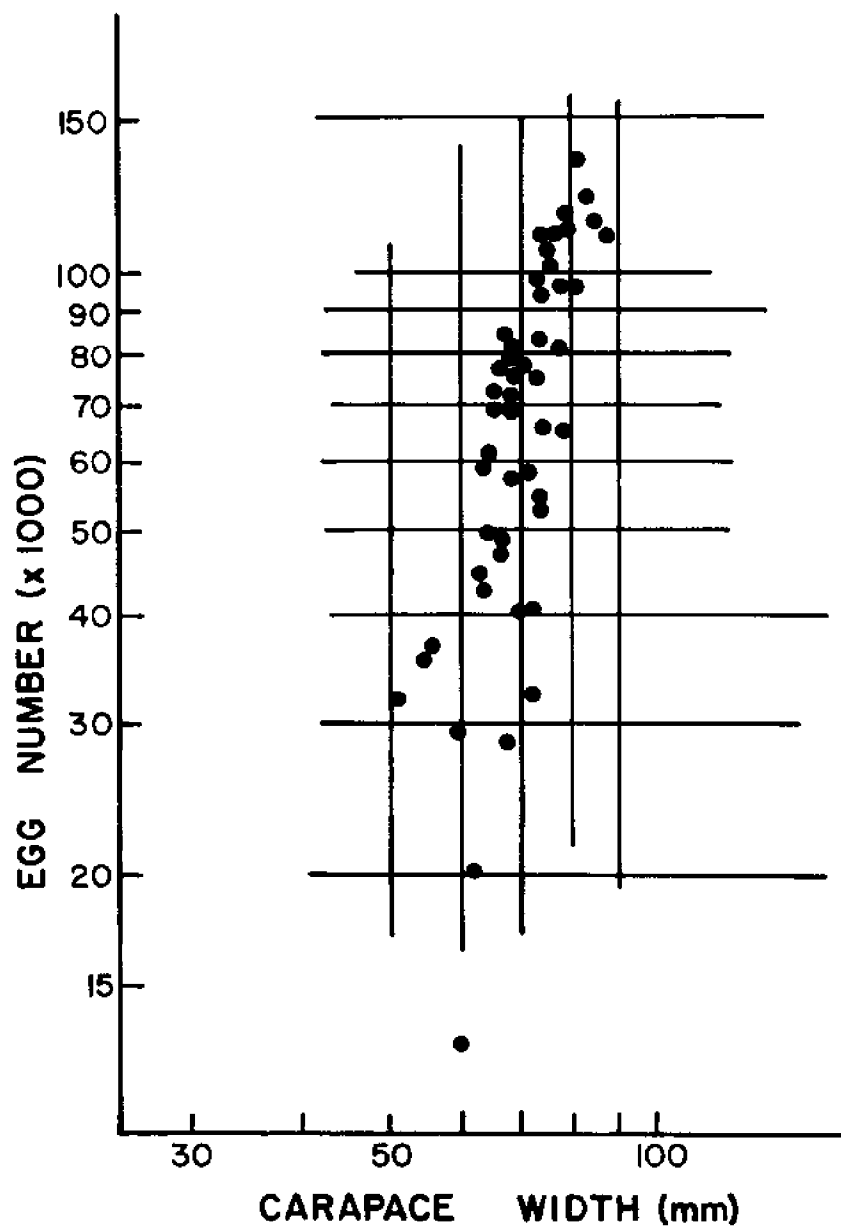
Figure 32. Number of eggs carried by female *C. opilio* (from Watson, 1969)
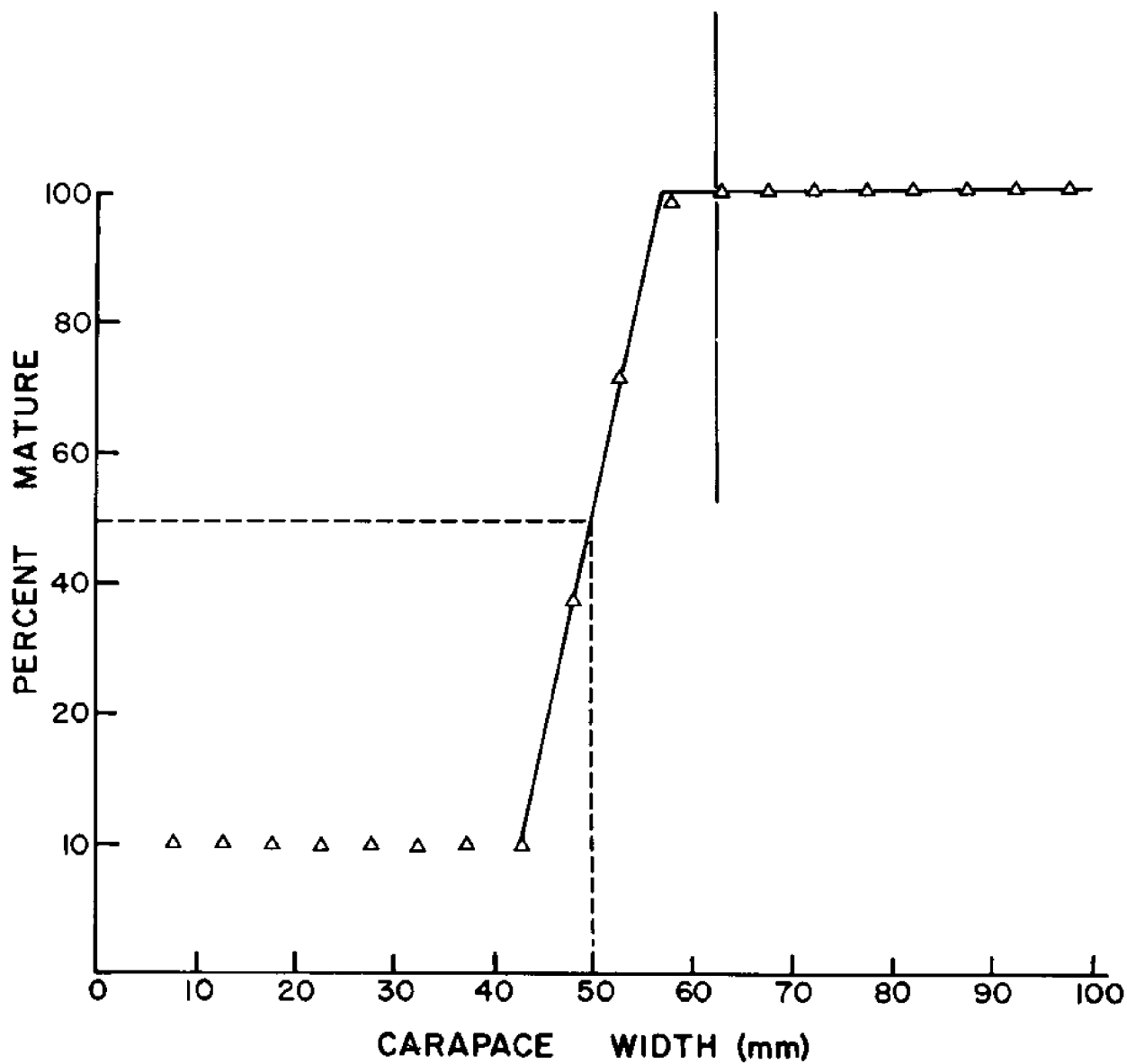
Figure 33. Relationship between percent maturity and carapace
width in female *C. opilio* (from Watson, 1969)
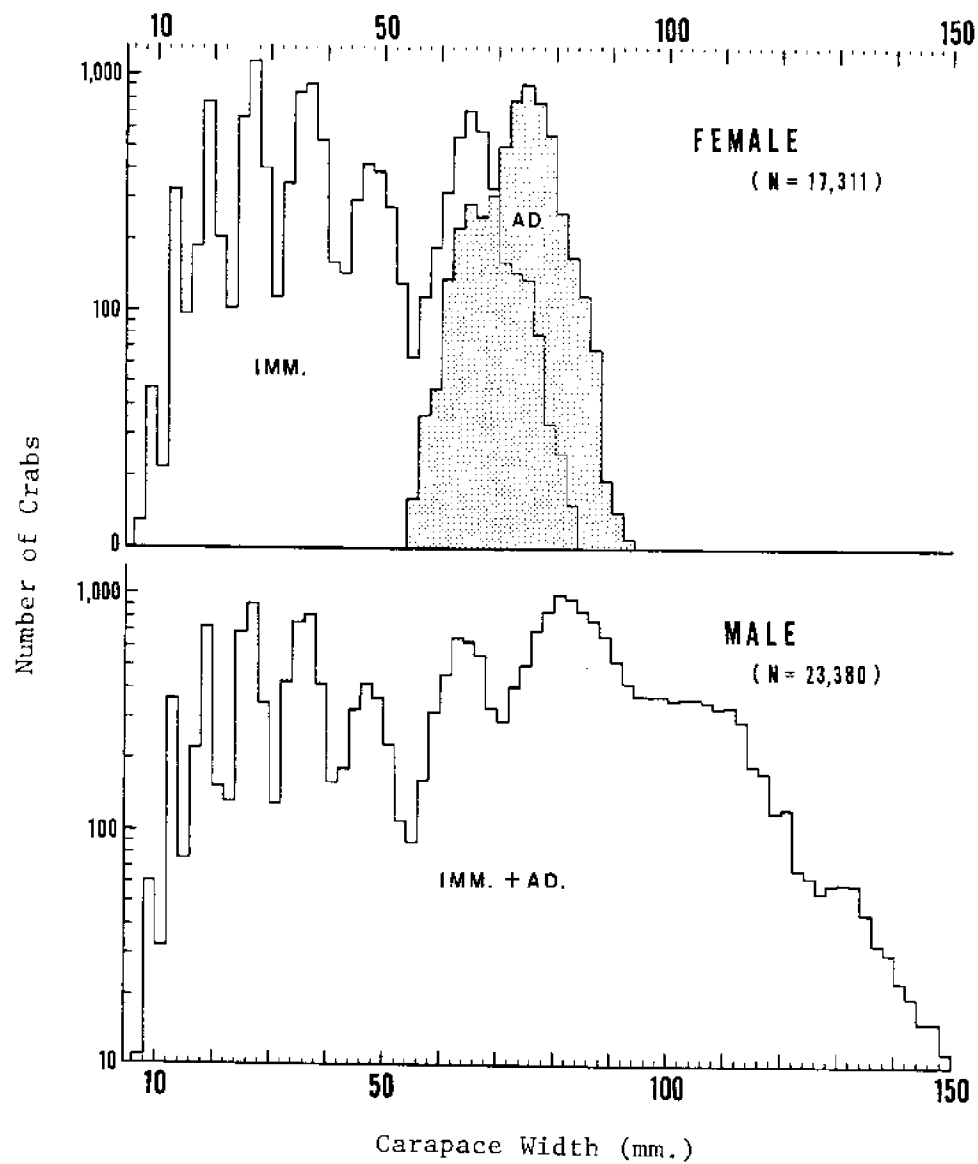
Figure 34. Carapace width frequencies by sex (from Ito, 1970)
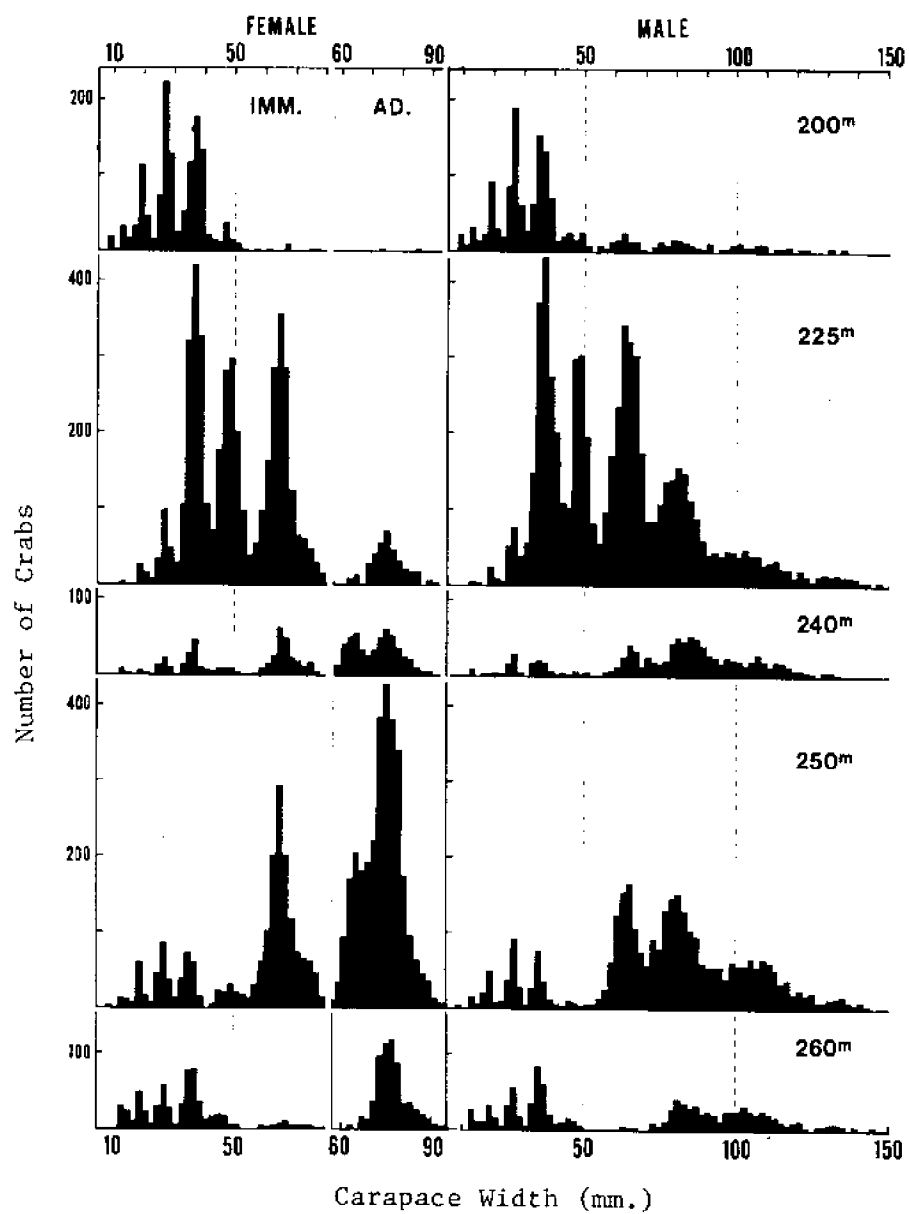
Figure 35. Carapace width frequency of *C opilio* by sex at depths 200 to 260 meters (from Ito, 1970)
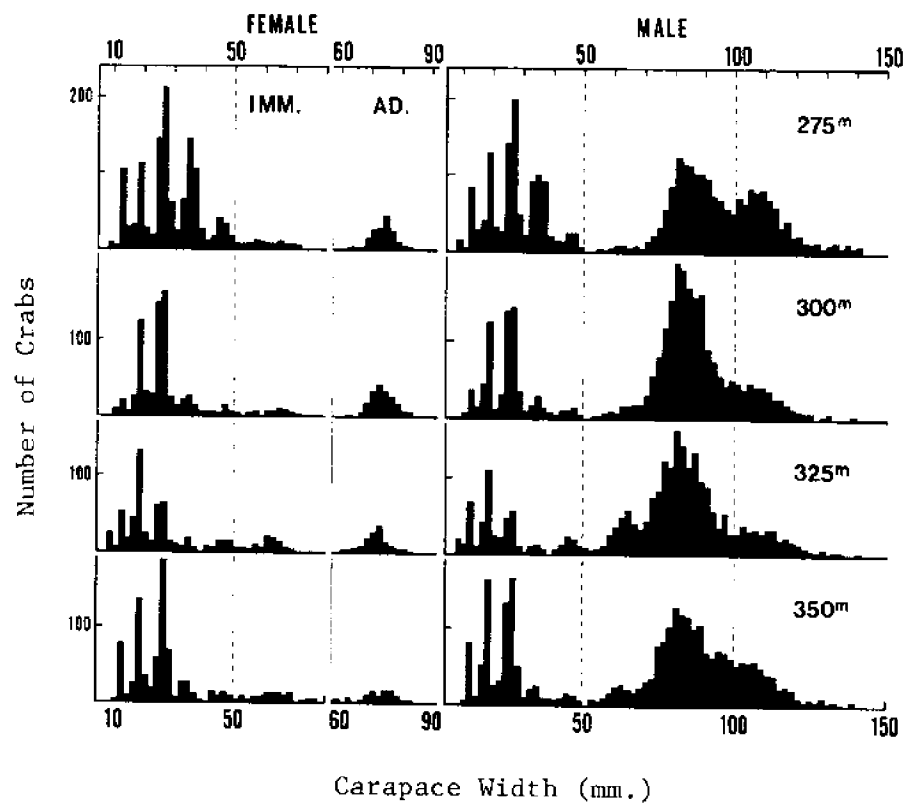
Figure 36. Carapace width frequency of *C. opilio* by sex at depths 275 to 350 meters (from Ito, 1970)
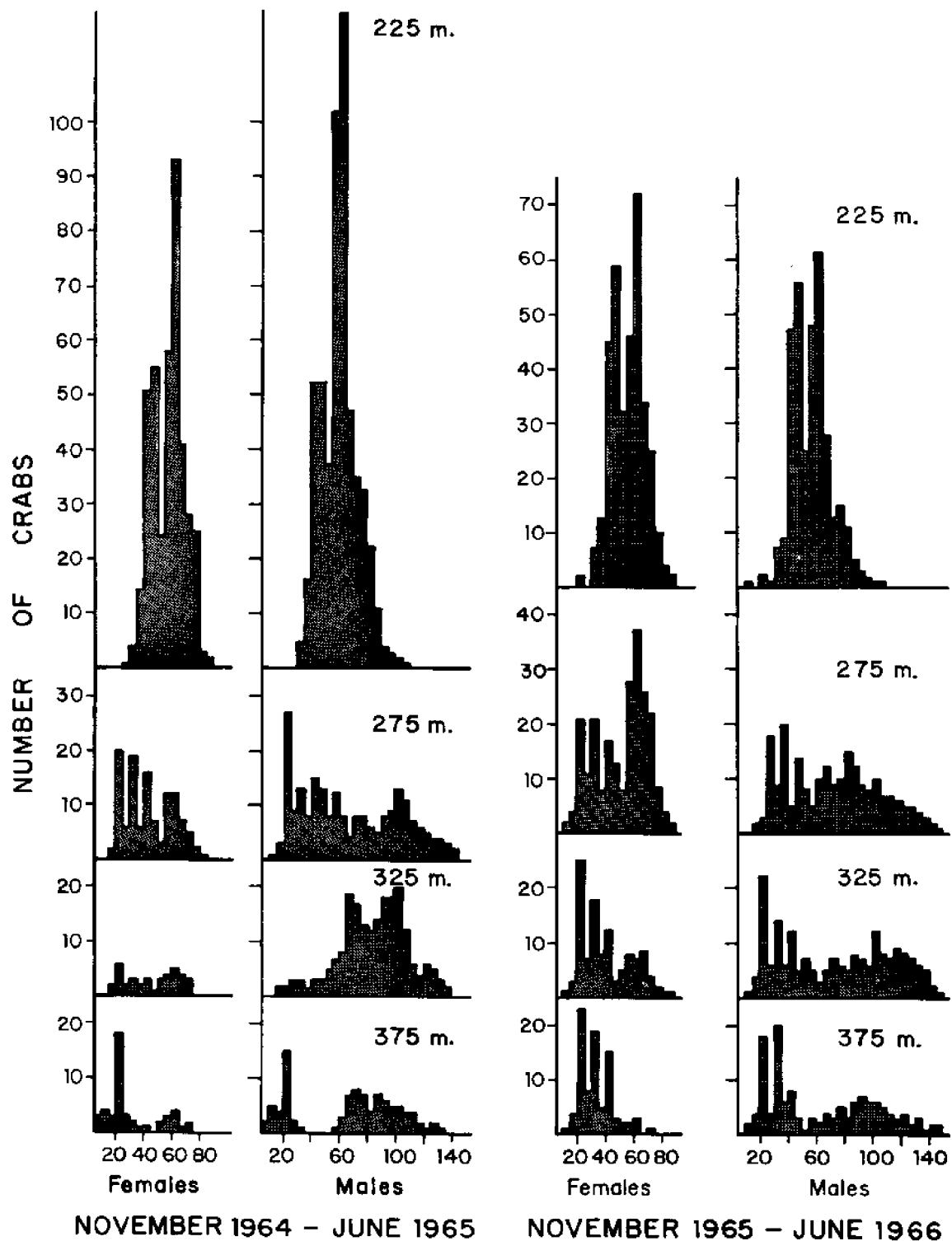
Figure 37. Frequency distribution of carapace widths of *Chionoecetes opilio* based on single trawls in each depth stratum (redrawn from Kon, 1969)
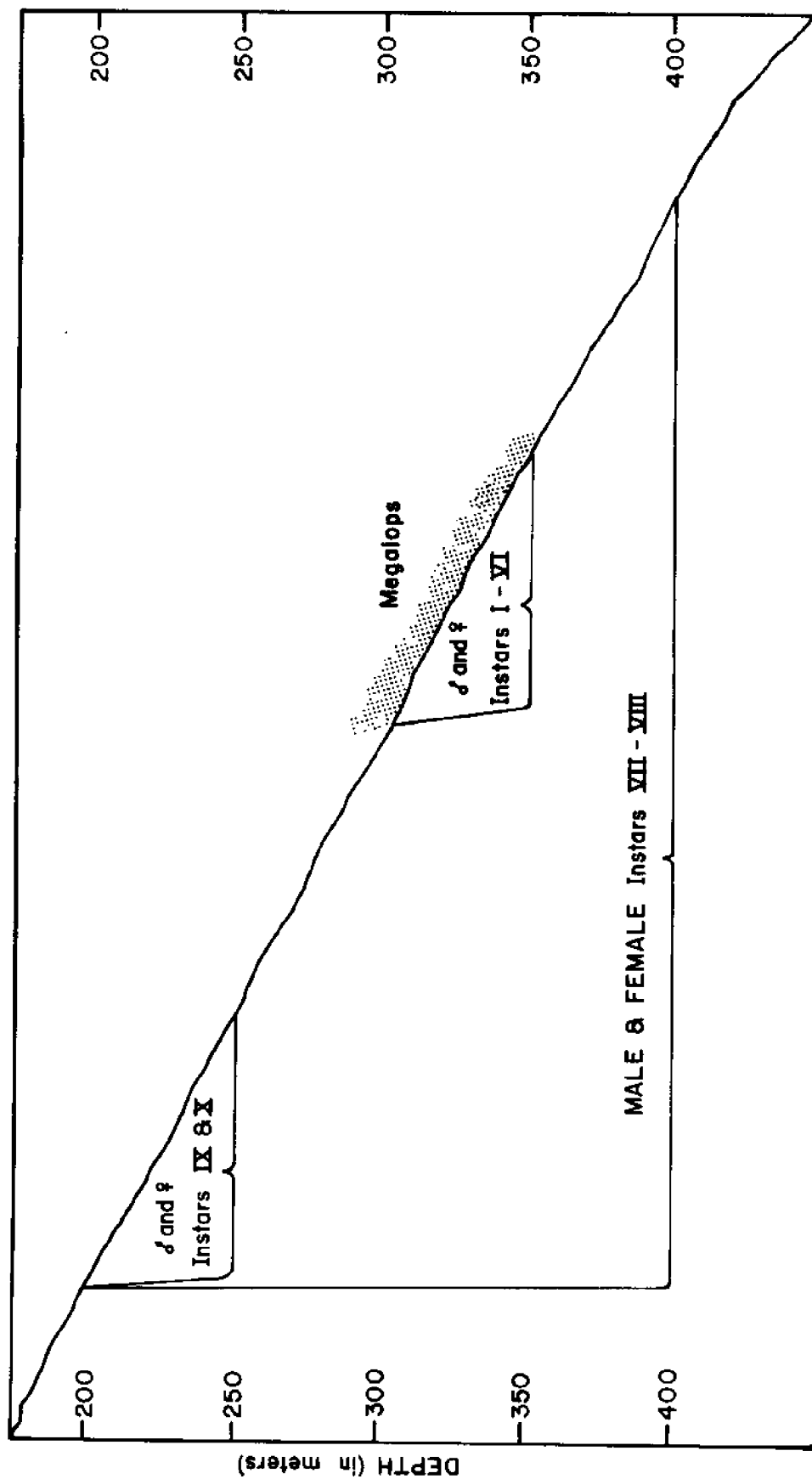
Figure 38. Depth distribution of megalops and instars of *Chionoecetes opilio* in the Sea of Japan (based on data from Kon, 1969 and Ito, 1970)
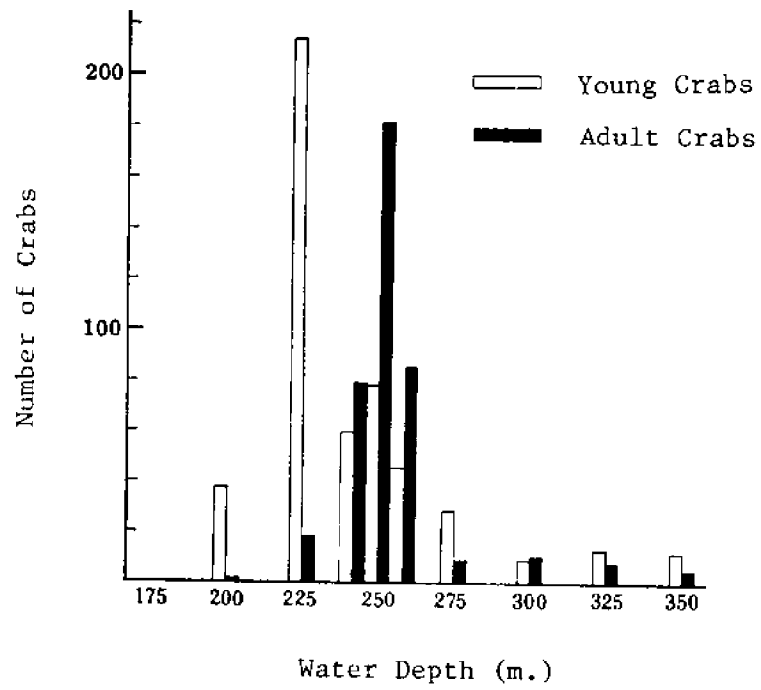
Figure 39. Average distribution of adult and young crabs per trawl at each depth (from Ito, 1967)
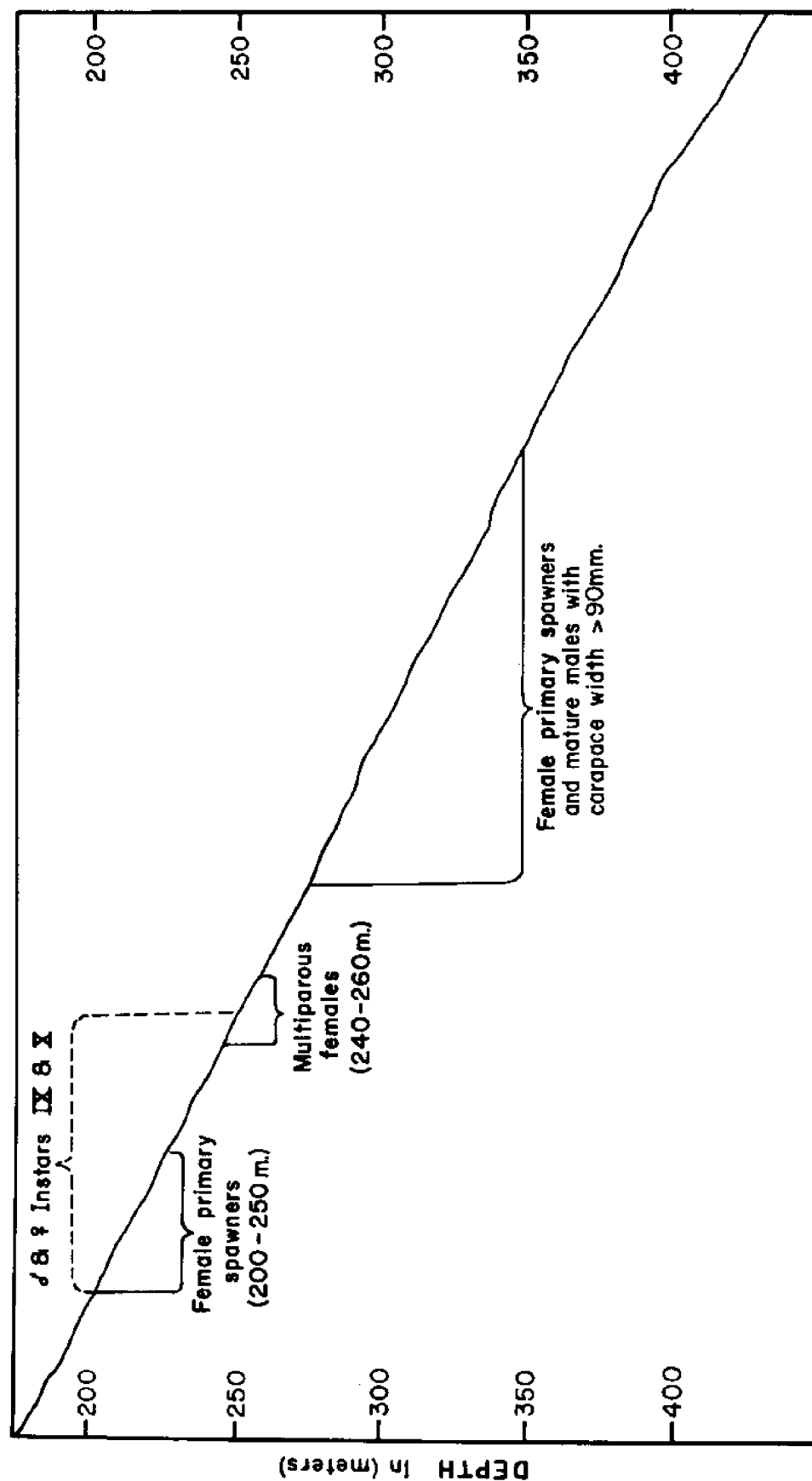
Figure 40. Depth distribution of last instars and adults of *Chionoecetes opilio* in the Sea of Japan (based on data from Kon, 1969 and Ito, 1970)
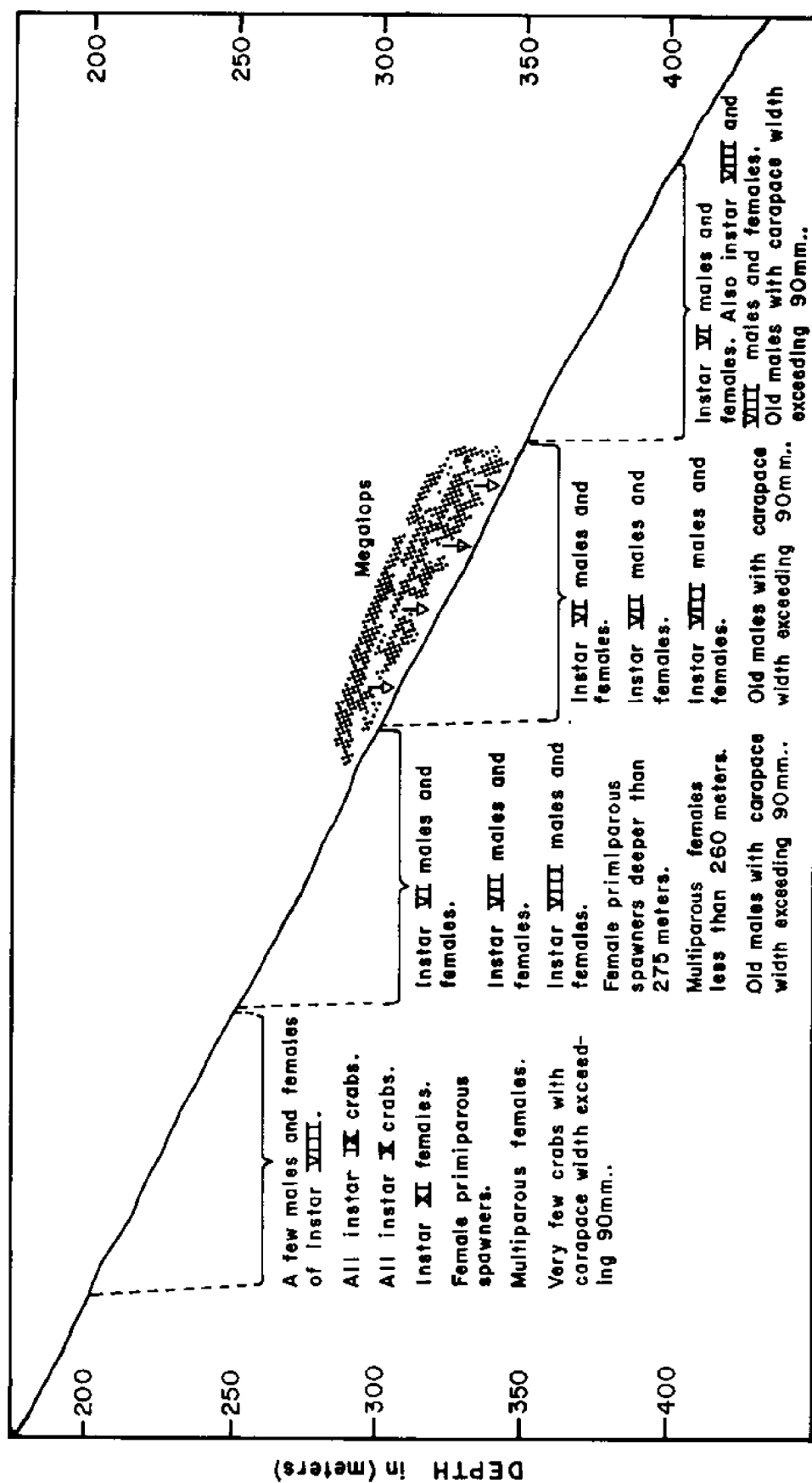
Figure 41. Depth distribution of all stages of megalops through adults of *Chionoecetes opilio* in the Sea of Japan (based on data from Kon, 1969 and Ito, 1970)
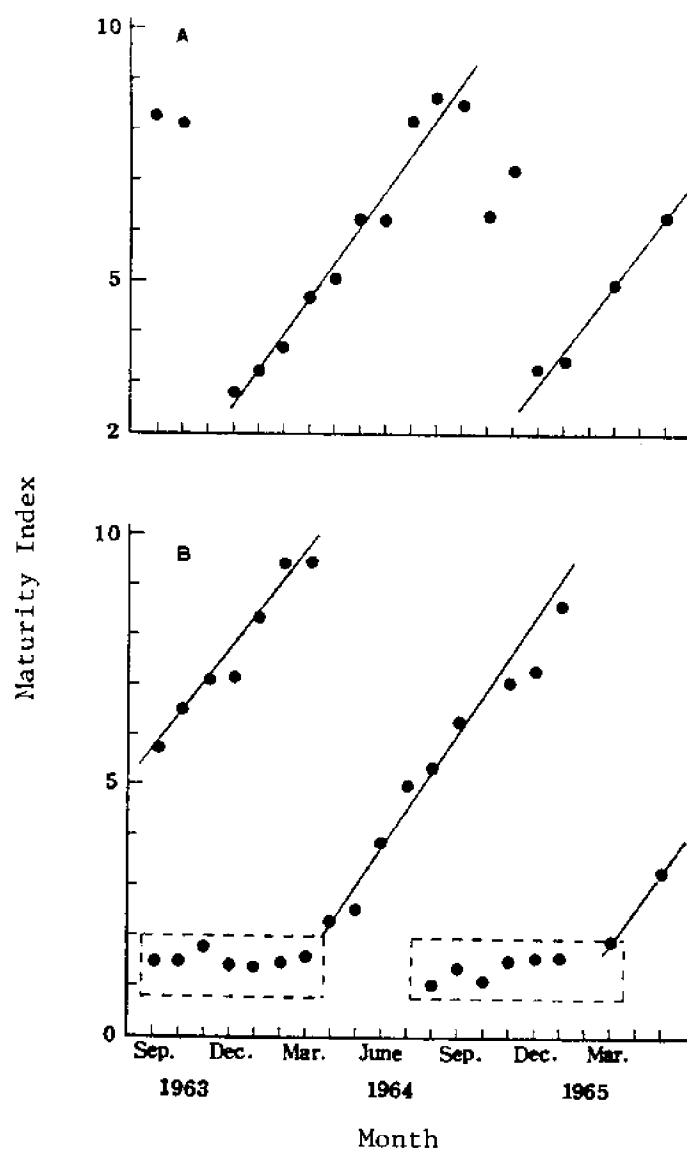
Figure 42. Monthly changes in the average maturity indices
of young crabs with rapidly maturing ovaries (A)
and of adult crabs (B) (from Ito, 1967)
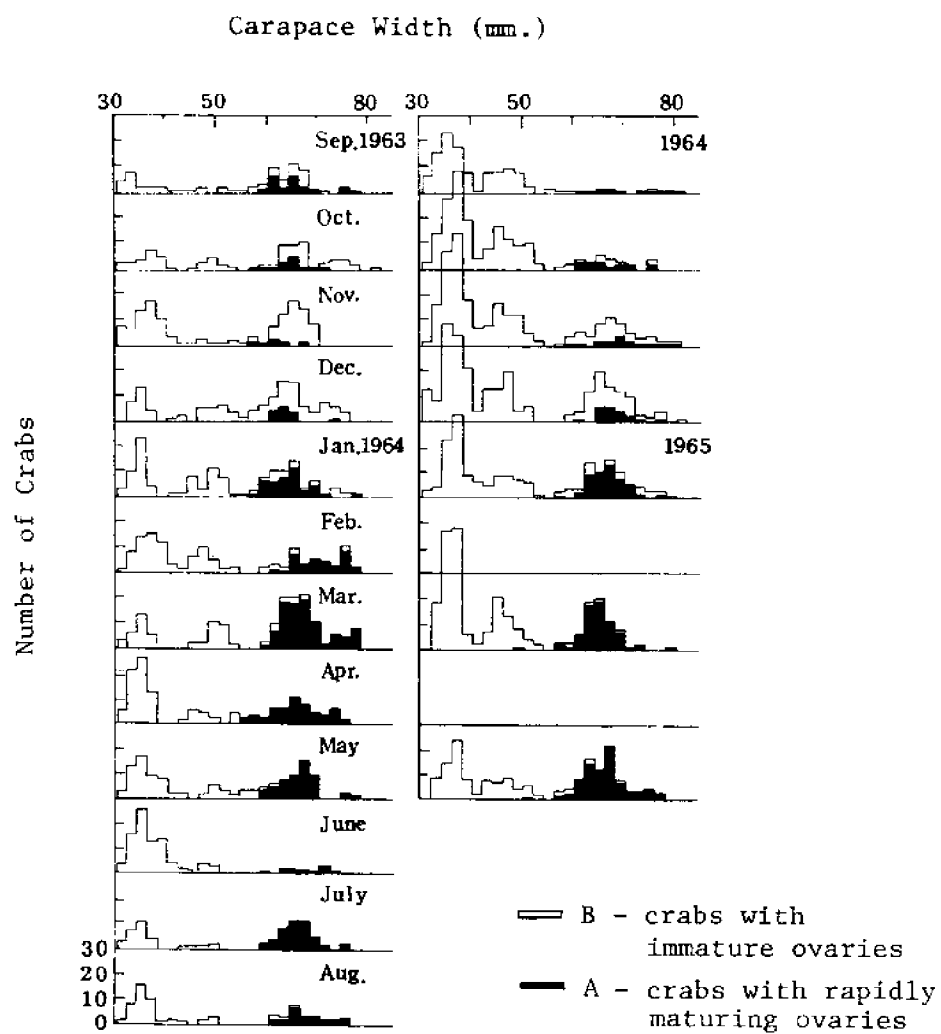
Carapace Width (mm.)

Figure 43. Seasonal changes in carapace width of young crabs in the Sea of Japan (from Ito, 1967)

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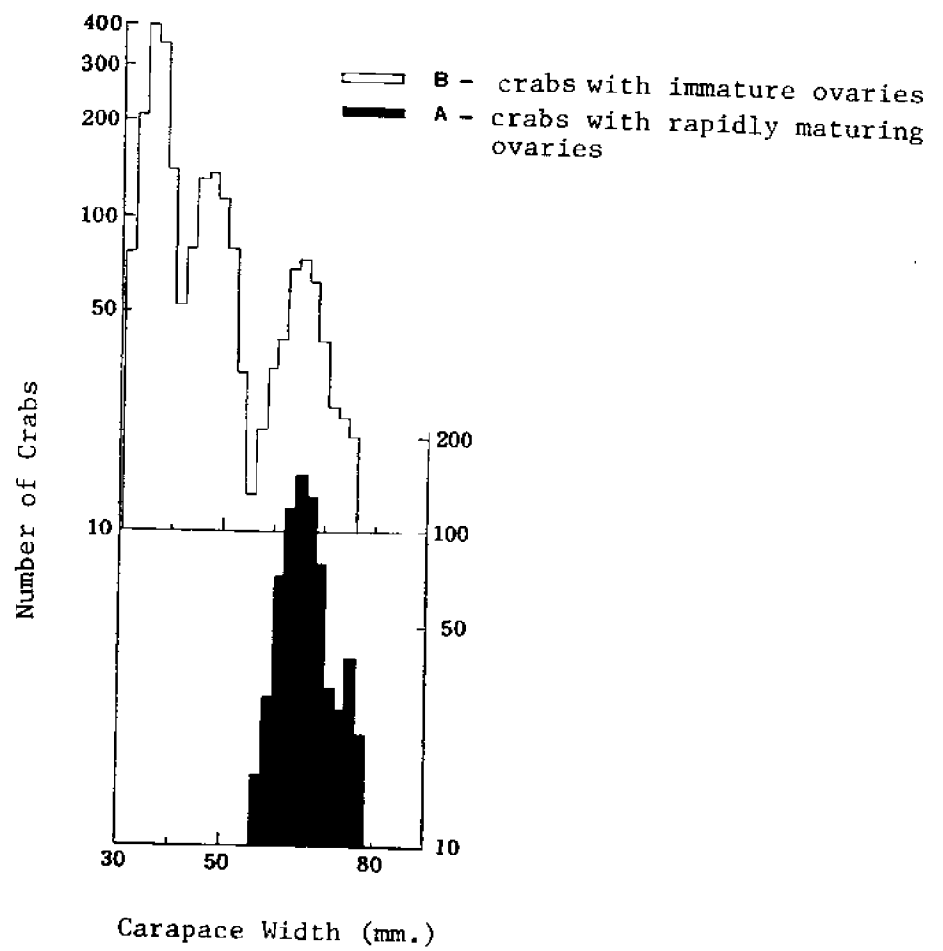
Figure 44.   Carapace width frequencies of female *C. opilio*
with immature ovaries (B) and with rapidly
maturing ovaries (A) (from Ito, 1967)
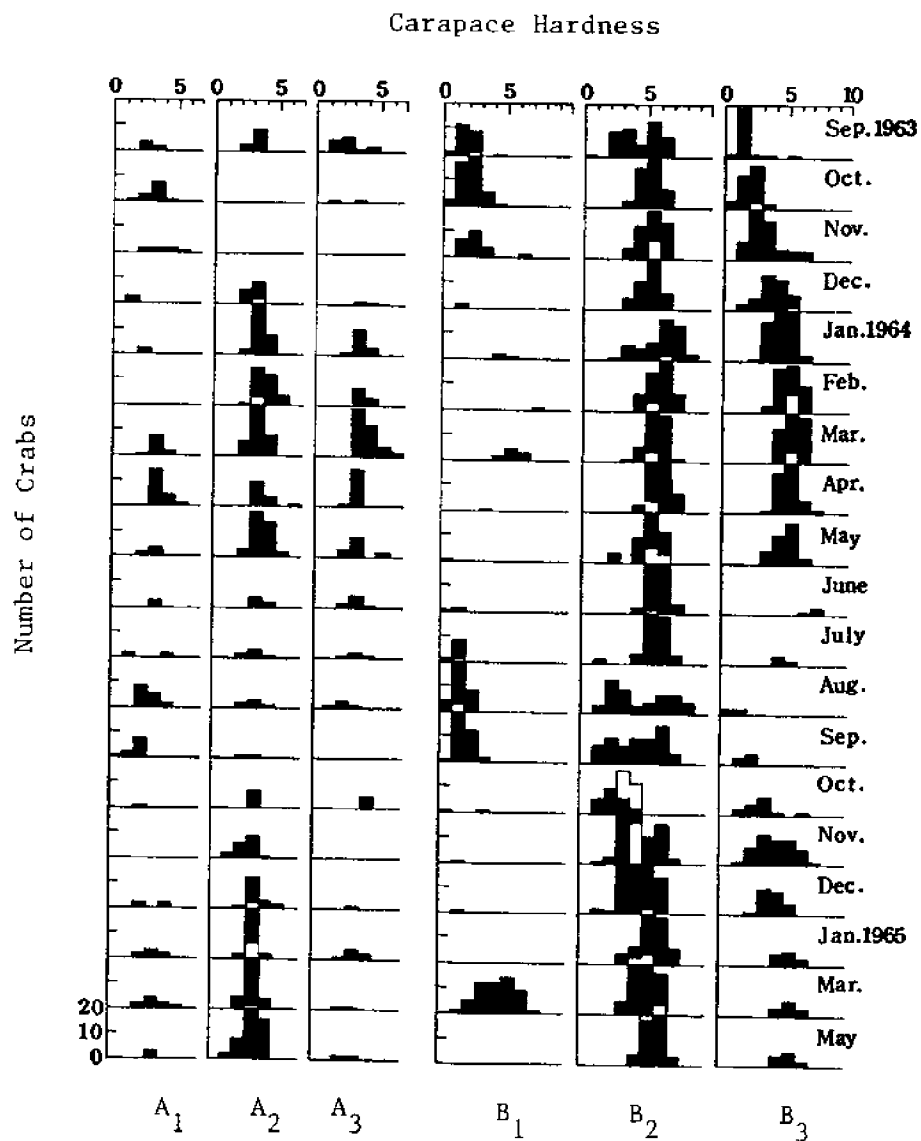
Carapace Hardness

Figure 45. Seasonal changes in carapace hardness of young crabs with
rapidly developing ovaries (A) and adult crabs (B) by depths
(from Ito, 1967). Subscripts 1, 2, and 3 refer to depth
zones: (1) 200-225 m; (2) 240-260 m; and (3) 275-350 m
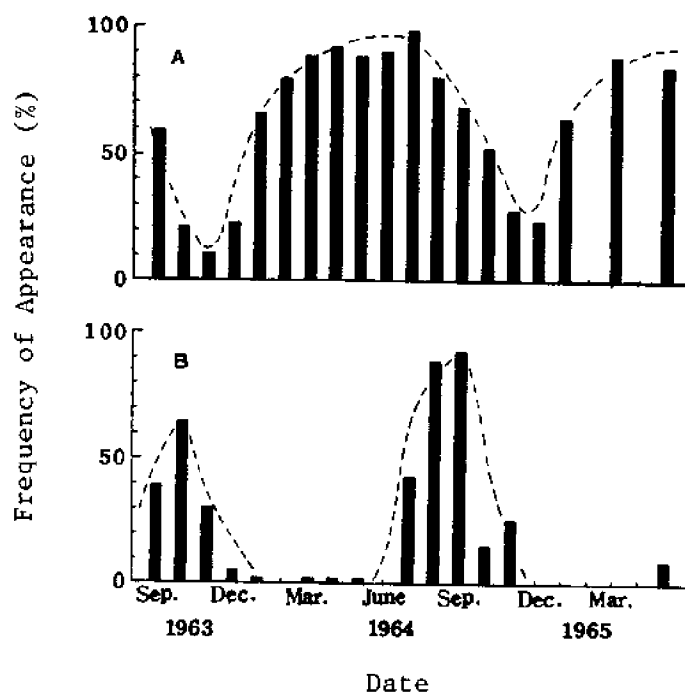
Figure 46. Seasonal changes in the frequency of appearance of
young crabs with rapidly maturing ovaries (A) and
double-carapaced crabs (B) (from Ito, 1967)
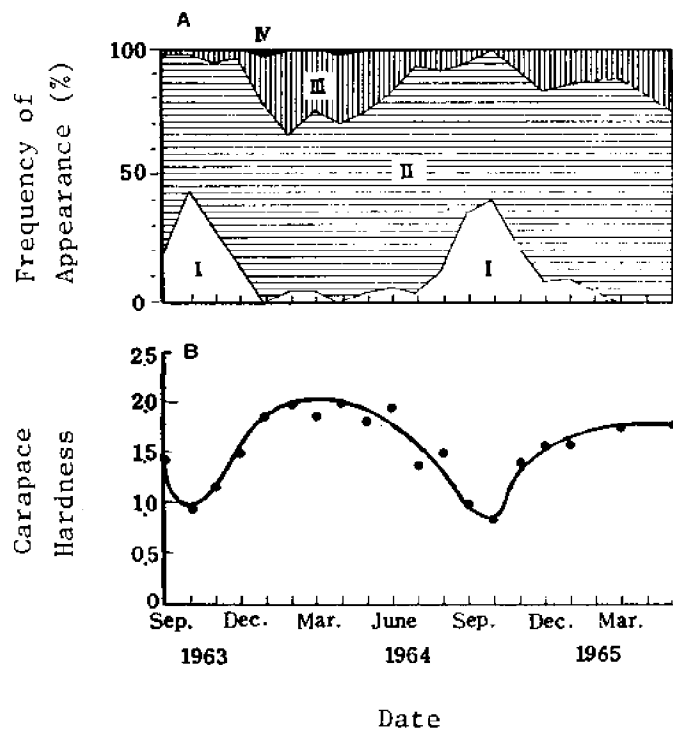
Figure 47. Seasonal changes in the frequency of occurrence
of young crabs (with rapidly maturing ovaries)
by differences in carapace hardness and monthly
changes in average hardness
A. Frequency of occurence by differences in hardness
I = Hardness 1.0 or less
II = Hardness 1.1 to 2.0
III = Hardness 2.1 to 3.0
IV = Hardness 3.1 to 4.0
B. Monthly changes in average carapace hardness
(from Ito, 1967)
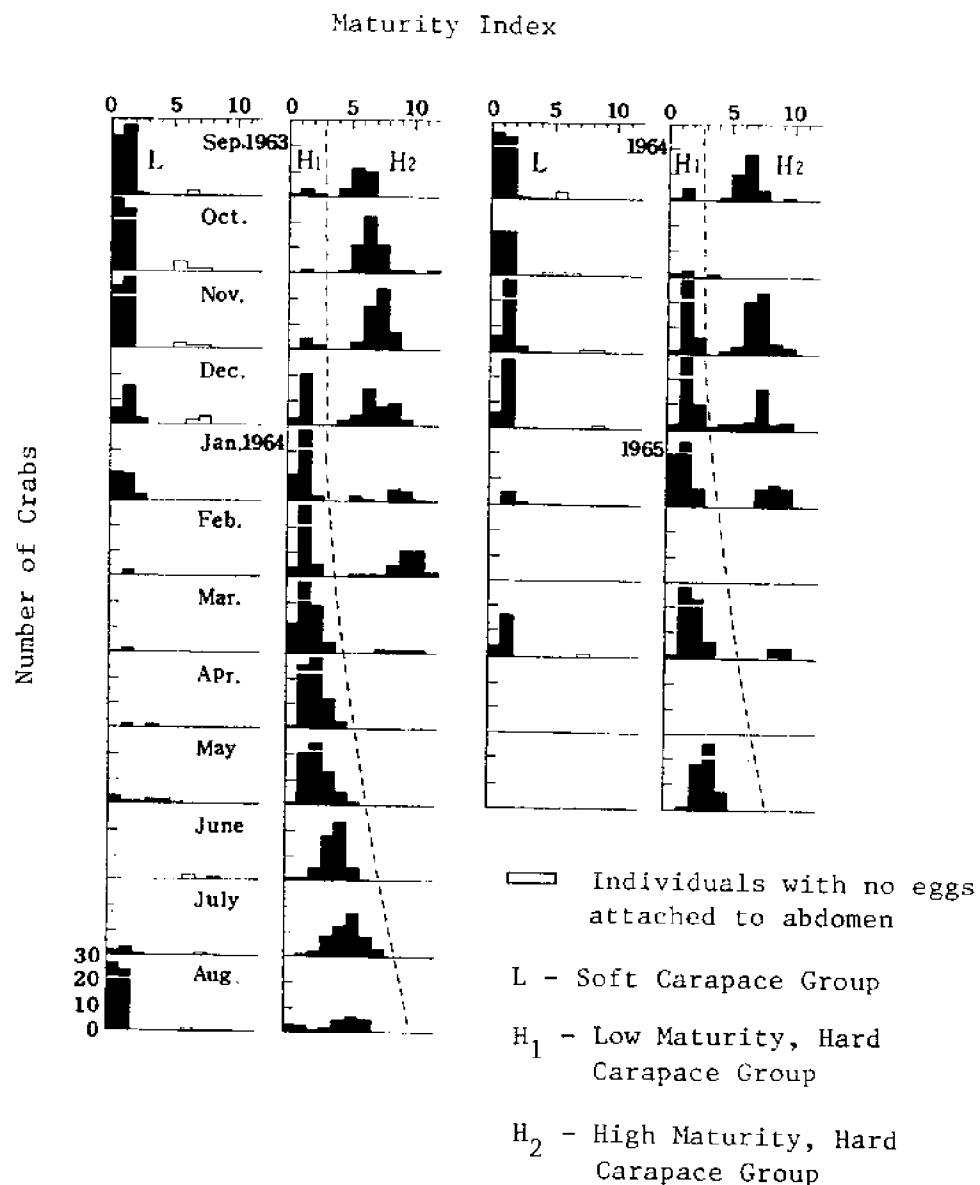
Maturity Index

Figure 48. Seasonal changes in the maturity indices of adult
crabs (from Ito, 1967). Please note that: (1)
Maturity Index values range from a minimum of 0 to
a maximum of 11; and (2) Ito states that group L
consists mostly of immature crabs with the
exception of a few individuals which have high M.T.
values in autumn.

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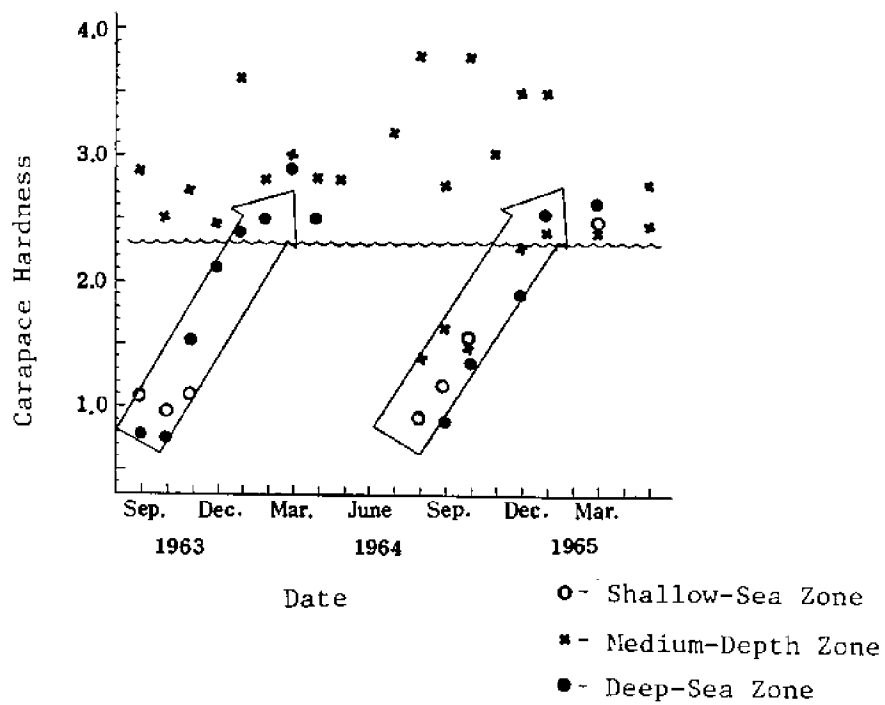
Figure 49. Seasonal changes in the average carapace hardness
of adult crabs by depths. The arrows indicate
seasonal trends in carapace hardness (from Ito,
1967)

Table 1. Occurrence of berried females and size distribution of *C. opilio* captured in traps off Gaspé, Quebec during July and August, 1968 (from Watson, 1969)

Depth (fathoms)			Catch per Trap Haul		
range	av.	Berried female	Soft	<4"	>4"
20–29	24	2.8	+	3.2	34.9
30–39	34	2.5	+	4.4	38.5
40–49	45	5.9	+	7.0	64.4
50–59	54	8.7	+	10.8	105.1
60–69	63	21.5	+	8.8	107.0
70–79	73	10.2	+	7.5	92.8
80–89	83	2.0	+	7.0	78.6
90–99	92	0	+	7.0	40.0
100–109	100	0	0	0	12.3
110–119	110	0	0	0	0
120–129	128	0	0	1.5	1.5

+ = <1 per trap haul.

Table 2. Development of *C. opilio* eggs

	Stage	Typical Color(s)
1)	Pre-eye forming stage (A-stage)	Orange and amber
2)	Early and intermediate eye-forming stage (B-stage)	Brownish-Yellow Reddish-brown, and Reddish-yellow
3)	Later eye-forming stage and the stage just prior to hatching (C-stage)	Dark brown, dark red, and purple
4)	Stage just prior to ovulation; eggs not yet attached to abdominal appendages (D-stage)	Deep brown (only the egg shell)

Table 3. Seasonal changes in the development of eggs attached to the abdominal appendages of *Chionoecetes opilio* (from Ito, 1967)

Month	Stage of Development*	High Maturity Soft Carapace			Low Maturity Hard Carapace		High Maturity Hard Carapace				
		A	D	Total	A	Total	A	B	C	D	Total
Sept., 1963		71	3	74	5	5	17	8	0	0	25
Oct.		80	3	83	1	1	18	29	0	0	47
Nov.		71	2	73	6	6	2	50	0	0	52
Dec.		25	3	28	18	18	1	44	0	0	45
Jan., 1964		23	0	23	67	67	0	9	3	0	12
Feb.		2	0	2	65	65	1	30	0	0	31
Mar.		1	0	1	115	115	1	0	3	1	5
Apr.		2	0	2	91	91	0	0	0	0	0
May		10	0	10	75	75	0	0	0	0	0
June		0	3	3	53	53	0	0	0	0	0
July		6	1	7	51	51	0	0	0	0	0
Aug.		67	1	68	25	25	0	0	0	0	0
Sept.		71	5	76	6	6	5	27	0	0	32
Oct.		34	3	37	3	3	1	0	0	0	1
Nov.		65	0	65	56	56	2	77	0	0	79
Dec.		33	0	33	71	71	2	27	0	0	29
Jan., 1965		4	0	4	40	40	1	18	3	0	22
Mar.		21	0	21	99	99	1	0	6	1	8
May		0	0	0	60	60	0	0	0	0	0

* Stages of development are as follows: A = Pre-eye-forming;
B = Early and intermediate eye-forming;
C = Late eye-forming stage through stage prior to hatching;
D = Unhatched eggs having no eyes (just prior to spawning).

Table 4. Appearance and length of larval stages of *Chionoecetes opilio*

Investigator & Date of Publication	Collection Area(s)	Year	Hatching Eggs and Prezoea	Zoea Stg. I	Stg. II	Megalops
Kurata (1963)	Hokkaido Area	1960 to 1962	–	March to June		April to May
Kurata (1963)	Sea of Okhotsk	"	–	May to July		July
Kurata (1963)	Pacific coast of Japan	"	–	August to Sept.		September
Kodaki (1965)	Sanriku on Sea of Japan	1963	–	––		June
Ito* (1967; 1970)	Kasumi on Sea of Japan	1963 to 1965	Feb. to April	February to May		June to February
			(Length of entire larval period 7-8 months and possibly as much as 9-10 months)			
Ito, Kasahara, Ikehara (1967)	Southwest Sea of Japan		–	April to May		April to May
Fukataki** (1965; 1969)	Various points along entire coast of Sea of Japan		–	March to May (1 month)	March to June (1 month)	April to June (3-6 months)
Yamahora (1969)	Yamagata		–	(27 days)	(27 days)	–
Fukui Prefecture Marine Experiment Station (1969)	–		–	(24-25) (days)	(24-25) (days)	(28 days)
Kon (1967; 1970)	Wakasa Bay on Sea of Japan	1969	(40-60 min.)	(19.0 days)	(20.4 days)	(27 days)
Takeuchi (1972)	Bering Sea	1961-1966		June	June to July	July

* All larval crabs examined by Ito were collected from the stomachs of the zoarcid, *Petroschmidtia toyamaensis* ("agogenge").

** Larval crabs examined by Fukataki were collected by net trawls and from the stomachs of *Onchorhynchus gorbuscha* ("Karafuto-masu") and *Onchorhynchus masou* ("Sakara-masu").

Table 5. Success of larval metamorphosis to the first zoeal stage at water temperature 5.3°C (from Kuwatani et al., 1971)

Date	Total No. of larvae metamorphosed		Time, min									
			0–20	20–40	40–60	60–80	80–100	100–120	120–140	140–160	160–180	180–200
1 Apr.	18	No.	3	9	0	2	3	1	0	0	0	0
		%	16.7	50.0	0	11.1	16.7	5.6	0	0	0	0
6 Apr.	67	No.	12	25	13	7	5	4	1	0	0	0
		%	17.9	37.3	19.4	10.4	7.5	6.0	1.5	0	0	0
13 Apr.	38	No.	4	8	6	10	5	3	1	1	0	0
		%	10.5	21.1	15.8	26.3	13.2	7.9	2.6	2.6	0	0
14 Apr.	24	No.	5	8	3	3	1	1	1	1	1	0
		%	20.8	33.3	12.5	12.5	4.2	4.2	4.2	4.2	4.2	0
16 Apr.	35	No.	2	20	3	2	3	3	1	0	1	0
		%	5.7	57.1	8.6	5.7	8.6	8.6	2.9	0	2.9	0
Average		%	14.3	39.8	11.3	13.2	10.0	6.5	2.2	1.4	1.4	0
Accumulated Total		%	0	54.1	65.4	78.6	88.6	95.1	97.3	98.7	100.1	100.1

Table 6. Appearance and survival of *Chionoecetes opilio* larvae as related to temperature in the natural environment and in rearing experiments (data from Kon, 1970)

STAGE OF DEVELOPMENT	LABORATORY REARING EXPERIMENTS					NATURAL ENVIRONMENT		
	Temp. Ranges Tested (°C)	Molting Success (%)	Time Required for Molt (Days)	Cumulative Water Temperature (Days °C)	Suitable* Temp. Ranges (°C)	Geographic Location	Surface Temperature at Time of Appearance (°C)	Temperature at Time of Largest Concentrations (°C)
ZOEA I	4.1-9.6	10-14	44-53	249.7-254.7	7-15	Sea of Japan	4 - 16	4 - 7
	7.9-12.9	52-57	22-28	221.9-240.0	(7.9-12.9)			
	10.0-17.1	34-40	15-20	224.7				
	15.5-17.0	25-48	10-17	224.9				
	16.5-18.8	33-39	10-14	215.4				
	18.9-19.8	0						
ZOEA II	4.2-7.2	46	53-61	299.3	7-15	Sea of Japan	4 - 17	4 - 14
	7.1-10.7	53-60	23-31	236.4	(7.1-10.7)			
	12.1-14.7	37-50	15-23	239.3-251.0				
	15.0-16.6	27-33	11-18	225.0-256.5				
	17.5-18.9	6-7	11-14	217.3-234.8				
MEGALOPS	8.5-14.0	7-8	26-30	261.7-314.7	12-17	Sea of Japan	1 - 17	10 - 11
	12.5-17.4	18-28	23-30	273.8-322.1	(12.5-15.0)			
	12.7-17.4	25	29	442.1				
LARVAL STAGES ZOEA I - MEGALOPS						Northeastern Hokkaido	-1.1 - 10.4	

*Optimum temperature is listed in parentheses.

Table 7. Duration of the intermolt period in the larval stages of *C. opilio* reared in vessels at different temperatures (from Kon, 1970)

Larval stage	Division of vessels	No. of first larva used	No. reaching next stage	Temp.(°C) Range	Temp.(°C) Mean	Intermolt period in days Range	Median	Integral temp. °C day
1	A	50	5	4.1~9.6	5.2±0.9	44~50	48	249.7
	B	100	14	4.1~9.6	5.2±0.9	44~53	49	254.7
2	A	44	25	7.9~12.9	9.6±1.1	22~25	23	221.9
	B	91	47	7.9~12.9	9.6±1.2	22~28	25	240.0
3	A	50	17	10.0~17.1	13.2±2.1	15~19	17	224.7
	B	100	40	10.0~17.1	13.2±2.1	15~20	17	224.7
4	A	48	12	15.5~17.0	16.1±0.5	13~16	14	224.9
	B	100	48	15.5~17.0	16.1±0.5	10~17	14	224.9
5	A	43	15	16.5~18.8	18.0±0.6	10~14	12	215.4
	B	93	36	16.5~18.8	18.0±0.6	10~14	12	215.4
6	A	40	0	18.9~19.8	--	--	--	--
	B	35	0	19.2~19.8	--	--	--	--
1´	C	26	12	4.2~7.2	5.2±0.6	53~61	57	299.3
2	A	25	15	7.1~10.7	8.7±1.3	26~29	27	236.4
	B	47	25	7.1~10.7	8.7±1.2	23~31	27	236.4
3´	C	28	14	12.4~14.7	13.3±0.6	15~22	18	239.3
	D	30	11	12.1~14.7	13.2±0.7	16~23	19	251.0
4	A	12	4	15.0~16.6	16.1±0.4	14~18	16	256.5
	B	48	13	15.0~16.6	16.1±0.4	11~17	14	225.0
5	A	15	1	17.5~18.9	18.1±0.4	13~14	13	234.8
	B	36	2	17.7~18.9	18.1±0.3	11~14	12	217.3
2	A	15	1	8.5~12.0	10.1±1.1	26	26	261.7
	B	25	2	8.5~14.0	10.5±1.3	29~30	30	314.7
3´	A	14	4	12.5~15.0	13.4±0.5	27~30	28	273.8
	B	11	2	12.5~15.0	13.4±0.6	23~24	24	322.1
4	A	4	1	12.7~17.4	15.2±0.9	29	29	442.1

Table 8. Aspects of the life history of *Chionoecetes opilio* O. Fabricius (data from Ito, 1970)

MOLTING GROUP	1	2 and 3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
ANIMAL FORM	PREZOEA	ZOEA I II	MEGALOPS	INSTAR I	INSTAR II	INSTAR III	INSTAR IV	INSTAR V	INSTAR VI	INSTAR VII	INSTAR VIII	INSTAR IX	INSTAR X	MALE ADULT I**	MALE ADULT II	MALE ADULT III
TIME AN INDIVIDUAL SPENDS IN THIS FORM	1 mo.	1 mo. / 2 months	5-10 mo.	3 mo.	3 mo.	3 mo.	3 mo.	6 mo.	13 mo.	12 mo.	12 mo.	12 mo.	12 mo.	12 mo.?	12 mo.?	?
MONTHS PRESENT	FEB. APR.	FEB. MAY	JUNE FEB.	OCT. MAY	JAN. JUL.	MAR. NOV.	JAN. NOV.	JAN. DEC. (Year Around)	YEAR AROUND	YEAR AROUND	YEAR AROUND	YEAR AROUND	YEAR AROUND	YEAR AROUND	YEAR AROUND	YEAR AROUND
MONTH(S) OF PEAK ABUNDANCE				FEB. MAY	FEB. JUNE	MAR. JUL.	OCT. NOV.	APR. JUL.								
CARAPACE WIDTH RANGE (in mm.)				2.4-3.4	3.6-5.0	5.2-7.8	8-12	10-16	14-24	22-32	28-46	38-56	52-74 (52-79)*	66-96 (54-92)*		
PEAK IN MOLTING ACTIVITY TO NEXT STAGE	MAR.	APR. MAY	OCT. FEB.	—	—	—	—	—	JUL. AUG.	JUL. SEPT.	JUL. SEPT.	AUG. NOV.	Males SEPT. NOV. / Females AUG. OCT.	Males DEC. DEC. / Females JUL. SEPT.	Males OCT. DEC.	OCT. DEC.

*Values in parentheses are for females.

**The three female instar molting stages which Ito believes undergo the terminal molt to maturity are the Instar X (Molting Group 14), and the Instar XI (Molting Group 15), and the Instar XII (Molting Group 16).

	15	16	17
	ADULT I	ADULT I	INSTAR XII
	OR	OR	ADULT I
	INSTAR XI	INSTAR XI	

Table 9. Duration of larval stages

Total Larval Period	Prezoea	Zoea I	Zoea II	Megalops	Author and Assumptions
63-66 days	40 - 60 minutes	19.0 days	20.4 days	27 days	Kon (1970). Average water temp. $12^{O}C$. Depth distribution less than 150 meters.
76-78 days	---	24-25 days	24-25 days	28 days	Fukui Pref. Marine Exp. Sta. (1969). Average water temp. $10-11^{O}C$.
----	---	27 days	27 days	---	Yamohara (1969). Average water temp. less than $10-11^{O}C$.
~5-8 months	---	~1 months	~1 months	~3-6 months	Fukataki (1969).
7-8 months	---	---	---	---	Ito (1970). Constant feeding habits for *Petroschmidtia toyamaensis*

Table 10. Carapace-width mode for each molting group

Author and Year of Publication	Study Area(s)	Number of Specimens	Study Years	1 Pre-zoea	2 Zoea I	3 Zoea II	4 Megalops	5 Instar I	6 Instar II	7 Instar III	8 Instar IV	9 Instar V	10 Instar VI	11 Instar VII	12 Instar VIII	13 Instar IX	14 Instar X	15 Adult I	16 Adult II	17 Adult III	18 Adult IV	19 Adult V	20 Adult VI	21 Adult VII
Kurata 1960, 1963	-	-	-	-	-	-	2.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sinoda 1968	Igumi (Hyogo Prefecture)	918 FF / 802 MM	Nov. 1966–Feb. 1967	-	-	-	-	-	-	-	-	-	-	-	-	41 (42)	65.5 (67.5)	76 / 74	91	109	132	-	-	-
Sinoda 1968	Kasumi (Hyogo Prefecture)	4,215 FF / 2,517 MM	Sept. 1963–July 1964	-	-	-	-	-	-	-	-	-	-	-	-	63 (66)	74 (75)	88	107.5	130	-	-	-
Sinoda 1968	Maizuru (Hyogo Prefecture)	8,714 FF / 4,953 MM	Oct. 1964–June 1965	-	-	-	-	-	-	-	-	-	-	-	-	62.5 (65)	75 (73)	92	110	131	-	-	-
Kon, Niwa, & Yamakawa 1968	Wakasa Bay Sea of Japan	12,155 FF / 17,097 MM	Nov. 1964–June 1965 and Nov. 1965–June 1966	-	-	-	-	3.1	4.6	6.5	9.7	13.5	19.6 (19.0)	27.3 (27.9)	36.8 (37.2)	49.2 (49.6)	65.2 (66.2)	(77.4)	-	-	-	-	-	-
Watson 1969	Chaleur Bay, New Brunswick Canada	.459	1968	-	-	-	-	-	-	6.5	9.7	13.5	19.6	27.3	36.8		65.2	78.0	91.0	104.0	114.0	125.0	137.0	151.0
Ito 1968, 1970	Kasumi (Hyogo Prefecture)	23,380 FF / 17,311 MM	Sept. 1963–May 1965	-	-	-	-	2.9–3.0	4.3–4.4	6.7	9–10 (9–10)	13–14 (13–14)	19–20 (19–20)	27–28 (27–28)	37–38 (37–38)	47–48 (47–48)	63–64 (65–66)	81–82 (75–76)	97–98 (82–84) or (85–86)	111–112	121–122	131–132	137–138	-
Kuwatami, Wakui & Nakanishi 1971	Hokkaido	-	1971	0.8 C.W. / 0.8 C.L.	1.0 C.W. / 1.2 C.L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Haynes 1973	Bristol Bay, Alaska	-	-	0.39 C.W.	0.54 C.L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Note: Carapace width modes in parentheses are those of female crabs.

FF = Females
MM = Males.

Table 11. Duration of the developmental stages of *C. opilio* (data from Ito, 1970 and Kon, 1970)

Ito, 1970

Prezoea ┐
Zoea I
Zoea II ├ Total larval life takes 7-8 or 9-10 months
Megalops ┘

Instar I ┐
Instar II
Instar III ├ All four total 12 months
Instar IV ┘

Instar V------ 6 months

Instar VI----- 13 months

Instar VII---- 12 months

All higher stages   Approx. 12 months

Kon, 1970

Prezoea ┐
Zoea I
Zoea II ├ Total larval life takes at most 3 months
Megalops ┘

Instar I ┐
Instar II ├ 12 months
Instar III ┘

Instar IV ┐
Instar V ┘ ├ 12 months

Instar VI ┐
Instar VII ┘ ├ 12 months

Instar VIII ┐
Instar IX ┘ ├ 12 months

Instar X-------- 12 months

Adult I----------- 12 months

Adult II---------- 12 months

Adult III-------- 12 months

Adult IV---------- 24 months

All higher stages   24 months

Table 12. Growth and age of *C. opilio* males (from Watson, 1969)

Pre-molt width mm	Post-molt width mm	Increment mm	%	Molt no.	Age	Source of data
2.2	3.1	0.9	-	-	1st Crab	Kon (1968)
Megalopa						
3.1	4.6	1.5	48	1		
4.6	6.5	1.9	41	2	1 yr	
6.5	9.7	2.2	34	3		
9.7	13.5	3.8	39	4	2 yr	
13.5	19.6	6.1	45	5		Kon (1968) and Watson (1969)
19.6	27.3	7.7	39	6	3 yr	
27.3	36.8	9.5	35	7		
36.8	49.2	12.4	34	8	4 yr	
49.2	65.2	16.0	33	9		
65.2	78.0	12.8	20	10	5 yr	Kon (1968)
78.0	91.0	13.0	18	11	6 yr	
91.0	104.0	13.0	15	12	7 yr	
104.0	114.0	10.0	10	13	9 yr	Hypothetical data
114.0	125.0	11.0	10	14	11 yr	
125.0	137.0	12.0	10	15	13 yr	
137.0	151.0	14.0	10	16	15 yr	

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Table 13. Seasonality of instar stages of *C. opilio* (data from Ito, 1970)

Stage of Development	Months Present	Months of Peak Abundance	Months of Peak Molting Activity*	
Instar I	October – May	February – May		
Instar II	January – July	February – June		
Instar III	March – November	March – July		
Instar IV	January – November	October – November		
Instar V	Year-round	April – July		
Instar VI	Year-round		July – August	
Instar VII	Year-round		July – September	
Instar IX	Year-round		August – November	
			Females	Males
			Aug.–Oct.	Sept.–Nov.
Instar X	Year-round			
Adult I				
(or Instar XI)	Year-round			

* As indicated by timing of the lowest value in carapace hardness.

Table 14. Growth model for *Chionoecetes opilio* immature males

MOLTING GROUP	PREZOEA	ZOEA I	ZOEA II	MEGALOPS	INSTAR I	INSTAR II	INSTAR III	INSTAR IV	INSTAR V	INSTAR VI	INSTAR VII	INSTAR VIII	INSTAR IX	INSTAR X
CARAPACE WIDTH: HYPOTHETICAL VALUE	<1	<1.2	1.5	2.2	3.0	4.5	6.6	9.5	13.5	19.5	27.4	37.3	49.0	63.7
CARAPACE WIDTH MODE VALUES IN LITERATURE	0.4 0.8	0.5 1.0	–	2.2	2.9-3.0 3.1	4.3-4.4 4.6	6.5-6.7	9-10 9.7	13-14 13.5	19-20 19.6	27-28 27.3	37-38 36.8	47-48 49.2 48 41	62-65 63-64 63-66
CARAPACE WIDTH RANGE VALUES IN LITERATURE	–	–	–	–	–	–	–	–	–	–	–	–	44.3-53.7 38-56	59.6-70.4 52-74
ABSOLUTE INCREMENT		~0.2	~0.3	~0.7	0.8	1.5	2.1	2.9	4.0	6.0	7.9	9.9	11.7	14.9
PERCENT INCREASE		16.7	20.0	31.8	26.7	33.3	31.8	30.5	29.6	30.8	28.1	26.5	23.9	23.0

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Table 15. Growth model for *Chionoecetes opilio* mature males

MOLTING GROUP	ADULT I	ADULT II	ADULT III	ADULT IV
CARAPACE WIDTH HYPOTHETICAL VALUES	77.7	91.4	111.2	132.4
CARAPACE WIDTH MODE VALUES IN LITERATURE**	81-82 78.0 76;75 74	84;85;91 85;88;91 92;93;96 97,97-98	103;103;104;117 105;107;109;118 110;111-112;114;119 115;115;115	121-122;123;124;124;140;143 125;126;127;128;130;143 131;131-132;135;136;143 137-138;137;140;140
CARAPACE WIDTH RANGE VALUES IN LITERATURE	66-96	83-112	92-124; 111-132	124-138; 132-142
ABSOLUTE INCREMENT	13.8	13.7	19.8	21.2
PERCENT INCREASE	18.0	15.0	18.0	16.0

** The values for mode in carapace width come from: Kon, et al. (1968); Ito (1968); Ito (1968 & 1970); Watson (1969); and Sinoda (1968). With slight modifications these data sets bear strong support for the results of more recent studies. The modifications were: 1. Watson's (1969) hypothetical values for molt numbers 13 and 14 were treated as two modes within a single molting group (Adult IV) and molt numbers 15 and 16 as two modes within the next higher molt (Adult IV); 2. Four of the molting groups described by Ito (1970) were combined to form only two molting groups. Therefore the Adult III stage includes crabs with carapace width ranges of 92-124 mm. and 111-132 mm.; the Adult IV stage includes crabs with carapace width ranges of 124-138 mm. and 132-142 mm. 3. With the latter change in mind, I arranged Sinoda's (1968) values (Table 10) into tentative molting groups. Organized in this manner, the hypothetical values for carapace width show a uniform increase (of approximately 18%) in size. Among adult crabs held in captivity, Miller and Watson (1976) found a uniform 18.4% increase in carapace width from one molting group to the next.

Table 16. Growth model for *Chionoectes opilio* females

MOLTING GROUP	PREZOEA	ZOEA I	ZOEA II	MEGALOPS	INSTAR I	INSTAR II	INSTAR III	INSTAR IV	INSTAR V	INSTAR VI	INSTAR VII	INSTAR VIII	INSTAR IX	INSTAR X	ADULT
CARAPACE WIDTH: HYPOTHETICAL VALUE	<1	<1.2	1.5	2.2	3.0	4.5	6.6	9.5	13.5	19.3	27.6	37.8	46.7	66.0	75.1
CARAPACE WIDTH MODE VALUES IN LITERATURE	0.4 / 0.8	0.5 / 1.0	–	2.2	2.9–3.0 / 3.1	4.3–4.4 / 4.6	6.5–6.7	9–10 / 9.7	13–14 / 13.5	19–20	27–28 / 27.9	37–38 / 37.2	49.8 / 47–48 / 42	66.2 / 65–66 / 67 / 66;65	77.4 / 75–76 / 74;75 / 73
CARAPACE WIDTH RANGE VALUES IN LITERATURE	–	–	–	–	–	–	–	–	–	–	–	–	45.2–54.2 / 38–56	60.3–72.1 / 54–92	72.0–82.8
ABSOLUTE INCREMENT	–	˜0.2	˜0.3	˜0.7	0.8	1.5	2.2	2.9	4.0	5.8	8.3	10.2	8.9	19.3	9.1
PERCENT INCREASE		16.7	20.0	31.8	26.7	33.3	31.8	30.5	29.6	30.0	30.1	27.0	19.0	29.0	12.0

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Table 17. Modes in carapace width increments for instar male and instar female
Chionoecetes opilio from Wakasa Bay in the Sea of Japan (data from Kon,
et al., 1968)

MALES

YEAR:	1964-1965 (N = 8714)	1965-1966 (N = 8383)	Average Values* (1964-65 + 1965-66/2)
	18.2 ± 1.6mm	20.0 ± 2.0mm	19.6 ± 1.8 mm
	27.0 ± 2.1	27.6 ± 2.2	27.3 ± 2.2
	36.8 ± 4.2	36.8 ± 2.9	36.9 ± 2.9
	49.4 ± 4.7	49.2 ± 4.7	49.0 ± 4.7
	65.4 ± 5.4	65.0 ± 5.4	65.0 ± 5.4

* Authors' quote: "There are five modes almost the same as the previous
year's result among the species collected during 1965 and 1966. The
numbers of modes below 65 mm are the same for both years." The maxi-
mum difference between any two corresponding modes is only 1.8 mm.
The authors made the assumption that the corresponding modes are the
same molting group. They then averaged the corresponding modes.

FEMALES

YEAR:	1964-1965 (N = 4953)**	1965-1966 (N = 7202)	Average Values (1964-65 + 1965-66/2)
	18.0 ± 1.5mm	20.0 ± 2.2mm	19.6 ± 1.8mm
	27.6 ± 2.3	28.2 ± 2.2	27.9 ± 2.3
	37.4 ± 3.8	37.0 ± 2.6	37.2 ± 3.0
	49.8 ± 4.6	49.4 ± 4.6	49.6 ± 4.6
	66.6 ± 5.9	66.6 ± 5.9	66.2 ± 5.9
	78.4 ± 4.6	76.2 ± 6.2	77.4 ± 5.4

** N indicates total sample size. Sample size for separate width-classes
was not described.

The average values from this table were entered in Table 18 which lists carapace
width modes for all instar stages of development.

Table 18. Modes in carapace width of *Chionoecetes opilio* as determined by Kon, Niwa, and Yamakawa (1968) for specimens from Wakasa Bay in the Sea of Japan

FEMALES		MALES	
CAPAPACE WIDTH (in mm)	MOLTING STAGE	CARAPACE WIDTH (in mm)	MOLTING STAGE
3.1 ± 0.2	INSTAR I	3.1 ± 0.2	INSTAR I
4.6 ± 0.4	INSTAR II	4.6 ± 0.4	INSTAR II
6.5 ± 0.4	INSTAR III	6.5 ± 0.4	INSTAR III
9.7 ± 0.6	INSTAR IV	9.7 ± 0.6	INSTAR IV
13.5 ± 1.5	INSTAR V	13.5 ± 1.5	INSTAR V
19.0 ± 1.8	INSTAR VI	19.0 ± 1.8	INSTAR VI
27.9 ± 2.3	INSTAR VII	27.3 ± 2.2	INSTAR VII
37.2 ± 3.0	INSTAR VIII	36.8 ± 3.3	INSTAR VIII
49.6 ± 4.6	INSTAR IX	49.2 ± 4.7	INSTAR IX
66.2 ± 5.9	INSTAR X	65.2 ± 5.4	INSTAR X
77.4 ± 5.4	ADULT	Males undergo additional molts as adults; however, the modes of these molting stages are difficult to determine.	

The values in this table are averaged values utilizing data from two years (see Table 17). Total sample sizes were as follows:

First year (Nov. 1964 – June 1965): 4953 Females; 8714 Males.

Second year (Nov. 1965 – June 1966): 7202 Females; 8383 Males.

Table 19. The range and mode of carapace widths in *Chionoecetes opilio* from the Sea of Japan (Kasumi, Hyogo Prefecture) as determined by Ito (1970)

FEMALES (N = 17,311)		MALES (N = 23,380)		
CARAPACE WIDTH MODE (in mm)	APPROXIMATE DATE OF MOLT	CARAPACE WIDTH MODE (in mm)	CARAPACE WIDTH** RANGE (in mm)	APPROXIMATE DATE OF MOLT
9-10		9-10	8-12	
13-14		13-14	10-16	
19-20	Apr. – June	19-20	14-24	Apr. – June
27-28	Jul. – Sept.	27-28	22-32	Jul. – Sept.
37-38	Aug. – Nov.	37-38	28-46	Aug. – Nov.
47-48	Aug. – Oct.	47-48	38-56	Sept. – Nov.
65-66	Jul. – Sept.	63-64	52-74(52-79)	Oct. – Dec.
75-76		81-82	66-96(54-92)	
82-84 or 85-86		97-98	82-112	
		Adult III { 111-112 / 121-122	{ 92-124 / 111-132	
		Adult IV { 131-132 / 137-138	{ 124-138 / 132-142	

The smallest carapace width mode listed above (9-10mm) is that of the instar IV stage. The figures continue through successive molt stages to a final instar XII stage for females and a final adult IV stage for males.

** Carapace width ranges for the first six molting groups listed by Ito are the same for both males and females. The seventh and eighth female molting group carapace ranges are listed in parentheses.

Table 20. Modes in maximum carapace width of *Chionoecetes opilio* (data from Sinoda, 1968)

	IGUMI AREA 918 males 802 females		KASUMI AREA 4,215 males 2,517 females		MAIZURU AREA 8,714 males 4,953 females	
	41	(42)			47.5	(50)
	65.5	(67.5)	63	(66)	62.5	(65)
	76	(74)	74	(75)	75	(73)
Adult II	85.2		84		85	
	91.0		88		92	
	96.0		93		97	
Adult III	103.5		103		105	
	109		107.5		110	
	115.5		115		115	
	118.5		117		119	
Adult IV	124		124		123	
	127		126.5		128	
	132		130		131	
	136.6		135		137.5	
	140.4		140		140	
	143.2		143		143	

Note: Numbers in the above table were read from Figures 3, 4, and 5 of Sinoda, 1968, and transcribed into the form of Table 20. Numbers in parentheses are carapace widths of females; all remaining values apply to male crabs only.

Table 21. Calculated values* of absolute increment and percent increase of carapace width by molting stage. (Read from top to bottom the values are: absolute increment – males; percent increase – males; absolute increment – females; percent increase – females.)

Molting Group	INSTAR II	INSTAR III	INSTAR IV	INSTAR V	INSTAR VI	INSTAR VII	INSTAR VIII	INSTAR IX	INSTAR X	ADULT I	ADULT II	ADULT III	ADULT IV
Ito Kasumi Area Sea of Japan 1968, 1970	1.40	2.35	2.8	4.0	6.0	8.0	10.0	10.0	16.0	18.0	16.0	14.0	18.7
	32.2	35.1	29.5	29.6	30.8	29.1	26.7	21.0	25.2	22.1	16.0	13.0	14.0
	1.40	2.35	2.8	4.0	6.0	8.0	10.0	10.0	18.0	10.0			
	32.2	35.1	29.5	29.6	30.8	29.1	26.7	21.0	27.5	13.2			
Kon, et al. Wakasa Bay Sea of Japan 1968	1.5	1.9	3.2	3.8	6.1	7.7	9.5	12.4	16.0				
	32.6	29.2	32.9	28.1	31.1	28.2	25.8	25.2	24.5				
	1.5	1.9	3.2	3.8	5.5	8.9	9.3	12.4	16.6	11.2			
	32.6	29.2	32.9	28.1	28.9	31.9	25.0	25.0	25.1	14.5			
Sinoda Igumi Area Sea of Japan 1968									24.5	10.5			
									37.0	10.5			
									25.5	6.5			
									38.0	9.0			
Sinoda Kasumi Area Sea of Japan 1968										11.0			
										15.0			
										9.0			
										12.0			
Sinoda Maizuru Area Sea of Japan 1968									15.0	12.5			
									24.0	17.0			
									15.0	8.0			
									23.0	11.0			

* Modal values of carapace width were used in these calculations. Values attributed to Sinoda (1968) were read directly from his figures 3, 4, and 5. 130.0 mm was used as an approximate modal value for the probable adult IV stage in Ito's data set. Ito recognizes three separate modes at 121–122 mm, 131–132 mm, and 137–138 mm, which I believe all belong to the adult IV stage.

Table 22. Growth equations for *Chionoecetes opilio*

AUTHOR AND YEAR OF PUBLICATION	GROWTH EQUATIONS	MOLTING STAGES USED IN CALCULATIONS. ADDITIONAL COMMENTS.
Sinoda 1968	$L_t = 164 \ (1 - e^{-0.97(t+2.73)})$ Where L_t = width in mm at t years of age	The author used Instar VI through Adult III stage males. Study area: off Hyogo Prefecture on the Sea of Japan He derived the equation from Von Bertalanffy's growth formula and parameters in the formula were estimated from Walford's diagram.
Ito 1970	$L_t = 180.4(1-e^{-0.165 \ (t-7.267)})$	The author used Instar X and older crabs to obtain values for the equation. Study area: off Kasumi, Hyogo Prefecture on the Sea of Japan
Powles 1966	$Y = 19X - 1510$ Where: Y = Body weight in grams; X = Caparace width in mm	81 crabs ranging in size from 100 to 150 mm carapace width and from 400 to 1300 grams body weight were used.
	C.W. = 1.013 C.L. Range: 1.00-1.03	52 crabs of carapace width ≤ 89 mm were used.
	C.W. = 1.024 C.L. Range: 0.99-1.03	72 crabs with carapace widths in the range 90 - 109 mm were used.
	C.W. = 1.028 C.L. Range: 1.01-1.06	79 crabs with carapace widths ≥ 110 mm were used.
	Where: C.W. = Carapace width C.L. = Carapace length	Study area: Gulf of St. Lawrence
Kanno 1972	$W = 0.00146 \cdot L^{2.762}$ Immature ♀ $W = 0.00430 \cdot L^{3.088}$ Mature ♀ $W = 0.00145 \cdot L^{2.806}$ Immature ♂ $W = 0.00304 \cdot L^{3.043}$ Mature ♂ Where: W = Body Weight; L = Carapace Length	Crabs that were used for obtaining values for equation derivation were Instar I through the largest adults. Study area: Okhotsk Sea
Kanno 1975	$L_t = 152 \ (1 + e^{2.31 - 0.399t})$	Crabs in the size range 9 to 134 mm were used. Study area: south Sakhalin area

Table 23. Supplementary growth equations for *Chionoecetes opilio*

AUTHOR AND YEAR OF PUBLICATION	GROWTH EQUATIONS	MOLTING STAGES USED IN CALCULATIONS. ADDITIONAL COMMENTS.
Kon, Niwa, and Yamakawa	Immature ♀ $L_{n+1} = 1.32L_n + 0.85$ Immature ♂ $L_{n+1} = 1.32L_n + 0.78$	For equations of immature growth, authors used modes of carapace width of Instars I through X.
1968	Mature ♀ $L_{n+1} = 0.67L_n + 32.7$ Where: L_{n+1} = Carapace width at the n+1 molting stage (or Post-molt).	The equation for growth of mature females was derived from the modes of carapace width of Instars IX, X, and XI
	L_n = Carapace width at the n molting stage (or Pre-molt).	Equation derived by use of Hiatt's Graph and Least Squares Method.
Ito 1970	Immature ♀ $L_{n+1} = 1.346L_n + 0.479$ Immature ♂ $L_{n+1} = 1.317L_n + 0.770$	Although not stated, author probably used modes of carapace width of Instars I through IX to obtain equations of immature growth.
	Mature ♀ $L_{n+1} = 0.800L_n + 23.100$ Mature ♂ $L_{n+1} = 0.848L_n + 27.428$	For mature growth Ito used the Instar X, Adult I (or ♀ Instar XI) and Adult II (or ♀ Instar XII).
		Equation derived by use of the Hiatt Graph and Least Squares Method.
Kurata 1960	$L_{n+1} - L_n = a(L_n - L_{n-1})$ Where "a" is "the common factor in a geometric series."	His model postulates that the growth rate in successive molting can be expressed by a geometric series. The value of growth coefficient a is >1 in both immature male and immature female crabs with an explosive growth pattern; while it is <1 in both mature male and mature female crabs with a converging growth pattern.
Ito 1968	$Y = 1.081 X + 1.340$ Where Y = carapace length in mm. X = carapace width in mm.	Instars I, II, and III used to obtain this equation.
Takeshita, Fujita, and Kawasaki	M.L. = 0.8322 C.W. − 1.5610	For growth equation of females, authors used 31 crabs with carapace widths in the range 54 − 66 mm.
1969	C.L. = 0.8183 C.W. + 2.8539 Where C.L. = Carapace Length C.W. = Carapace Width	For growth equation of males, authors used 66 crabs with carapace widths in the range 58 − 134 mm.
	M.L. = Merus Length	Study area: Eastern Bering Sea.

Table 24. Test of significant difference by covariance analysis for the slope and position of allometric lines between populations in two fishing grounds (east coast of southern Sakhalin and off Monbetsu, Hokkaido) in 1970 (from Kanno, 1972)

Body parts (to carapace width)	Area	Number of specimen	Two constants k	Two constants log b	Slope difference (F)	Positional difference (F)
Chelate leg	Monbetsu	63	1.244	−0.690	1.63	6.57*
	East saghalien	46	1.146	−0.473		
2nd ambulatory leg	Monbetsu	63	1.047	−0.056	1.29	20.04**
	East saghalien	46	0.978	0.064		
3rd ambulatory leg	Monbetsu	62	0.976	0.089	2.11	18.74**
	East saghalien	46	0.937	0.157		
4th ambulatory leg	Monbetsu	61	0.957	0.078	1.33	23.35**
	East saghalien	44	0.902	0.167		
5th ambulatory leg	Monbetsu	62	0.954	−0.125	2.69	6.75*
	East saghalien	46	0.849	0.084		
1st abdominal segment	Monbetsu	63	0.754	−0.286	4.60*	11.09**
	East saghalien	46	0.845	−0.478		
2nd abdominal segment	Monbetsu	63	0.908	−0.421	0.00	1.17
	East saghalien	46	0.913	−0.435		
3rd abdominal segment	Monbetsu	63	0.915	−0.376	1.48	2.09
	East saghalien	46	0.953	−0.446		
4th abdominal segment	Monbetsu	63	0.877	−0.218	1.71	5.77*
	East saghalien	46	0.928	−0.315		
5th abdominal segment	Monbetsu	63	0.891	−0.227	1.36	5.52*
	East saghalien	46	0.907	−0.253		
6th abdominal segment	Monbetsu	63	0.885	−0.264	1.05	0.00
	East saghalien	46	0.921	−0.341		
Distance between orbits	Monbetsu	63	0.867	−0.107	1.88	0.94
	East saghalien	45	0.849	−0.066		
Body weight-carapace width relation	Monbetsu	63	3.181	−3.761	1.31	0.01
	East saghalien	46	3.074	−3.549		

* Significant at the 5% level
** Significant at the 1% level

Name of fishing ground	Location Lat.	Location Long.	Date of capture	Method of capture
Southern Saghalien	47°45'	145°15'	'70-9-14	crab-trap
Off-shore of Monbetsu	45°26'	143°50'	'70-11 14	crab-trap

Table 25. Allometric growth in *C. opilio* males. Equilibrium constant κ and the constant log *b* in the allometric formula $y = bx^{\kappa}$, where y and x are length of body parts and carapace width (from Kanno, 1972)

(male)

Body parts	Stage	Number of specimen	κ	log *b*	
Chelate leg	1st	34	1.000±0.047	-0.380	isauxesis
	2nd	27	1.254±0.060	-0.711	tachyauxesis
2nd ambulatory leg	1st	34	0.954±0.033	0.022	bradyauxesis
	2nd	27	1.078±0.060	-0.149	isauxesis
3rd ambulatory leg	1st	34	0.935±0.037	0.080	bradyauxesis
	2nd	27	0.993±0.085	0.017	isauxesis
4th ambulatory leg	1st	34	0.885±0.035	0.128	bradyauxesis
	2nd	27	1.062±0.132	-0.175	isauxesis
5th ambulatory leg	1st	34	0.785±0.051	0.110	bradyauxesis
	2nd	27	1.062±0.101	-0.370	isauxesis
1st abdominal segment		61	0.898±0.020	-0.590	bradyauxesis
2nd abdominal segment	1st	34	1.054±0.028	-0.708	tachyauxesis
	2nd	27	0.918±0.067	-0.441	isauxesis
3rd abdominal segment	1st	34	1.132±0.030	-0.780	tachyauxesis
	2nd	27	0.939±0.058	-0.421	isauxesis
4th abdominal segment	1st	34	1.101±0.027	-0.655	tachyauxesis
	2nd	27	0.953±0.057	-0.368	isauxesis
5th abdominal segment	1st	34	1.141±0.026	-0.683	tachyauxesis
	2nd	27	0.953±0.047	-0.349	isauxesis
6th abdominal segment		61	1.026±0.018	-0.548	isauxesis
Distance between orbits	1st	45	0.746±0.017	-0.119	bradyauxesis
	2nd	16	0.924±0.119	-0.222	isauxesis
Body weight-carapace width relation	1st	34	2.806±0.069	-3.161	
	2nd	27	3.043±0.138	-3.483	

Table 26. Size at maturity of female *C. opilio* from the Gulf of St. Lawrence
(from Powles, 1966)

	Below 60mm Carapace Width	60mm or more Carapace Width	Total
Berried	1	99	100
Not Berried	9	7	16
% Berried	10%	93%	86%

Table 27. The longevity and size at maturity for *Chionoecetes opilio*

Author and Year of Publication	Study Area	Number of Specimens	Longevity	Size and Age of Maturity
Yoshida 1941		—	—	Males ~66 mm carapace width
Powles 1966	Cape Breton Island, Nova Scotia; Gaspé, New Brunswick	116 FF*	—	Females ~60 mm carapace width
Kon, Niwa and Yamakawa 1968	Wakasa Bay Sea of Japan	12,155 MM** 17,097 FF	—	Females ~77 mm carapace width
Sinoda 1968	Sea of Japan off Igumi, Kasumi & Maizuru	8,272 FF 13,847 MM	Females live to ~16 or 17 years	Females ~75 mm carapace width or at age 6 or 7
Kon 1969	Wakasa Bay Sea of Japan	16,700 MM 11,908 FF	—	Males ~75 mm carapace width Females ~77 mm carapace width
Watson 1969	Chaleur Bay New Brunswick	143 MM 38 FF	Males live to ~15 years	Males begin to mature at 55 to 65 mm carapace width. The vas deferens, based on 30 specimens, is fully mature at carapace width 60 to 70 mm (age 5). At ~50 mm carapace width, 50% of the females were mature.
Ito 1970	Kasumi (Hyogo Prefecture) Sea of Japan	23,380 MM 17,311 FF	Males reach approximately 138 mm carapace width at 20th molt or 12.5 years age. One male measuring 174 mm carapace is recorded; its estimated age is 18-19 years. Females have 3-4 years of mature life. Estimated female longevity is 11 or 12 years.	The total carapace width range of Adult I males is 66 to 96 mm. Females attain sexual maturity at 6 to 8 years of age; the total carapace width range of mature females is 54 to 92 mm.
Watson 1970	Gulf of St. Lawrence	—	—	At 57 mm carapace width, 50% of the males were sexually mature.

*FF = Females

**MM = Males

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Table 28. The molting stages of Brachyura (after Knowles and Carlisle, 1956 and Lockwood, 1967)

STAGE A Immediately after molting. No feeding.

    Substage A_1 Exoskeleton is a soft membrane hence the crab is incapable of supporting itself on its limbs. Water is being absorbed; therefore, weight is unstable.

    Substage A_2 Mineralization of the cuticle commences and, although the exoskeleton is still soft, the crab can now stand. Water content of the whole crab is 86 percent and the weight is stable.

STAGE B The main period of cuticle calcification which entails increased absorption of calcium and reduction of the water content. No feeding.

    Substage B_1 Secretion of the calcareous layer begins. The meropodite and propodite of the legs can be bent without breaking. Water content 85 percent.

    Substage B_2 Continued secretion of the exoskeleton. Meropodite and propodite will crack if bent. Water content 83 percent.

STAGE C Longest period in the molt cycle. The cuticle is hard and calcification gradually ceases during the early substages. Feeding is resumed. Water is slowly replaced by tissue.

    Substage C_1 The major period of tissue growth. Opposite broad faces of the legs give slightly if squeezed. Water content 80 percent.

    Substage C_2 Tissue growth continues. Opposite faces of the limbs yield under slight pressure but crack if firmly pressed. Water content 76 percent.

    Substage C_3 Integument of the legs is completely rigid; however, the lateral and frontal areas of the carapace are slightly translucent since calcification in these regions is not yet complete. Water content 68 percent.

    Substage C_4 The intermolt stage; longest substage in the cycle. An inner membranous layer adheres to the shell which is now completely calcified. Tissue growth is complete and metabolic reserves are accumulating. Water content 61 percent.

STAGE D Preparatory stage for the forthcoming molt. Calcium resorption occurs and the outer layers of a new cuticle are secreted. Feeding ceases and metabolic reserves are mobilized. After substage D_2 the crab becomes less active. Water content 59 to 61 percent.

    Substage D_1 The impending molt is first indicated by formation of new setae at the base of the old ones. A new epicuticle is secreted by the hypodermis.

    Substage D_2 The new pigmented layer is secreted.

    Substage D_3 Extensive re-absorption of calcium along the line of dehiscence results in a gaping in the cuticle. Water uptake begins.

STAGE E The crab escapes from the old shell and swells as water is rapidly taken up.

Table 29. Variations in the carapace condition of *C. opilio* (from Powles, 1966)

Condition	Ventral Color	Dorsal Color	Epibiotics	Remarks
S	Dead white or pink	Pale brown and green	None	Animal is weak; legs easily bent and broken.
H_1	White or pink	Light, bright brown and green	None	Spines and rostral horns sharp and well defined; small spots of brown on legs against pale green background.
H_2	Dirty white or yellow	Dark brown and green	Start to appear	Spines and rostral horns slightly worn.
H_3	Dark yellow to light brown	Very dark brown	Plentiful	Spines and rostral horns quite worn and dull; mossy encrusting substance on dorsal surfaces of carapace and legs.

Explanatory comments for tables 30 and 31. Maturity and molting cycles of
C. opilio

Tables 30 and 31 are based on information presented by Ito (1967) which was
accumulated during a two year study in the Sea of Japan near Kasumi (Hyogo
Prefecture). This particular study examined only female specimens of *C. opilio*.
Ito uses a number of indices (referred to in the tables) which are explained
below:

1. Carapace Hardness....Using Mokuya's Scale of Fruit-Hardness
    graduated by 0.1 kilogram units to the maximum of 5 kg, Ito
    found a maximum carapace hardness of less than 4 kg. There-
    fore, he established eight grades of 0.5 kg each. The lowest
    possible value was hardness 1.0 and the highest possible
    value was 8.0.

2. Maturity Index....The formula used in the determination of
    Maturity Index was: M.I. = (GW/BW - FW) x 100.

    Where GW = the weight of the ovary in grams
          FW = the weight of eggs attached to the abdomen (g)
          BW = the body weight in grams

    Since the minimum M.I. value was smaller than 12.0, twelve
    gradations were established from the lowest of M.I. = 0
    to the highest of M.I. = 11.

It is important to keep in mind the fact that the tables illustrate trends in the
development of most females. Individual crabs do not all undergo these changes
at precisely the same time; therefore, some variation is to be expected from the
general trends.

Arrows in the table indicate trends in development. Dashed lines indicate a
change or reversal in the trend.

Table 30. Carapace condition and molting cycles of female *Chionoecetes opilio* in the Sea of Japan (data from Ito, 1967)

OCT.	NOV.	DEC.	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.

INSTAR VIII

Peak carapace hardness — Carapace softens — Molt to Instar IX

2.1 to 3.0 — Oct. to Nov.

INSTAR IX

Carapace hardens — Carapace softens — Molt to Instar X — Aug. to Nov.

INSTAR X

Carapace hardens — Carapace softens — Molt to Maturity — Aug. to Sept.

APPEARANCE AND CARAPACE CONDITION OF
DEVELOPMENTAL STAGES FROM
INSTAR VIII TO ADULT:

ANNUAL OCCURRENCE OF "DOUBLE-SKIN" CRABS:

– – – – Lowest Frequency – – – –   – – – Peak Frequency – ● – –

CHANGES IN CARAPACE HARDNESS OF
FEMALE INSTARS DURING PART OF
THE YEAR:

Shallow Sea Zone (200 - 225m)
and
Deep Sea Zone (275 - 350 m)

Hardness 0.8 from August to October → Hardness peaks at 6.0 in February

CHANGES IN CARAPACE HARDNESS OF
PRIMIPAROUS SPAWNERS DURING
PART OF THE YEAR:

Medium depth Zone (240 - 260 m) Group 1

Hardness 2.0 in September → Hardness peaks at 6.0 in February

CHANGES IN CARAPACE HARDNESS OF
MULTIPAROUS FEMALES DURING PART
OF THE YEAR:

Medium Depth Zone (240 - 260 m) Group 2

Hardness remains 5.0 to 6.0 between September and February. Average yearly carapace hardness for this group is 2.3 to 3.8.

Table 31. Maturation of female *Chionoecetes opilio* in the Sea of Japan (data from Ito, 1967)

OCT. NOV. DEC. JAN. FEB. MAR. APR. MAY JUNE JULY AUG. SEPT. OCT. NOV.

INSTARS I through VIII

MATURITY INDEX OF EARLY INSTARS WITH SOFT CARAPACES:

M.I. = 1.0. Most soft-carapaced instars have slowly maturing ovaries which show very little seasonal change in ripeness.

ANNUAL CHANGES IN RATIO OF INSTARS WITH RAPIDLY MATURING OVARIES/ INSTARS WITH SLOWLY MATURING OVARIES:

Ratio Decreases   Ratio Increases   Ratio Decreases

INSTAR IX | ADULT

OVARIAN DEVELOPMENT OF CRABS FROM THE INSTAR IX STAGE TO THIRD ADULT OVULATION:

Low Maturity   Ovaries Maturing   Maximum Maturity | Primary Spawning   Ovaries Resting
M.I. = 1.0   M.I. = 9.0 to 10.0

Ovaries Resting .... Ovaries begin to Mature

M.I. 9.0 to 10.0   Low Maturity Ovaries Begin to Mature
Second Ovulation

M.I. 9.0 to 10.0
Third Ovulation

OCT. NOV. DEC. JAN. FEB. MAR. APR. MAY JUNE JULY AUG. SET. OCT. NOV.

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Table 32. Depth distribution of *Chionoecetes opilio* by sex in the Sea of Japan (data from Kon, 1969)

STRATUM NO.	II	III	IV	V
DEPTH RANGE	200 – 250 m	250 – 300 m	300 – 350 m	350 – 400 m
	FEMALES	FEMALES	FEMALES	FEMALES
	Almost all were $\geq$ 45mm in carapace width. No smaller crabs were found.	Full range of carapace widths were present. Many crabs had carapace widths between 20 and 45mm or > 90 mm.	Full range of carapace widths represented. Those with carapace $\geq$ 60mm were considerably less common. Total number of crabs decreased.	Juveniles predominated. carapace width sizes > 15 mm were present and sizes 20–45mm were most abundant. Total number of crabs was small. Carapaces $\geq$ mm were negligible compared with Stratum II. Small crabs, in the size range 15–20 mm, were uncommon.
	MALES	MALES	MALES	MALES
	Almost all were 45–85mm in carapace width. No smaller crabs were found.	Carapace widths in the entire range of 20–140 mm were present. Many crabs had carapace widths between 20 and 45mm or $\geq$ 90mm.	Full range of carapace widths were represented. Total number of crabs decreased.	Juveniles were numerous. Range of carapace widths the same as in Stratum IV. Those with carapace width $\geq$ 90mm were less common than in other strata but consistently appeared. Small crabs, in the size range 15–20mm, were uncommon.

The following note applies to both males and females: Very few crabs were found with carapace width exceeding 90mm. Those with a carapace width exceeding 100mm were especially rare. Carapace widths in the range of 45 to 85mm were predominant and the numbers of crabs collected in Stratum II re-presented 60 to 80 percent of the total sample from all strata.

Table 33. Depth distribution of *Chionoecetes opilio* by maturity in Wakasa Bay in the Sea of Japan (data from Kon, 1969)

IMMATURE CRABS

STRATUM II	STRATUM III	STRATUM IV	STRATUM V
200 - 250 m	250 - 300 m	300 - 350 m	350 - 400 m

6th molting stage: Carapace width = 15-20mm

7th molting stage: Carapace width = 25-30mm

A few 8th molting stage crabs were taken in Stratum II.

8th Molting Stage: Carapace width = 35-40mm

9th molting stage: Carapace width = 45-50? mm

MATURE CRABS

STRATUM II	STRATUM III	STRATUM IV	STRATUM V
200 - 250 m	250 - 300 m	300 - 350 m	350 - 400 m

200-250 m
10th and 11th molting stages

240-260 m
Mature females.
There is some seasonal migration by females to shallower water but not as often as similar migrations by males.

275-400 m
Mature males > 90mm in carapace width. Males do exhibit seasonal mating migrations to shallower water.

Table 34. Straight line distance travelled from release point to capture location by *Chionoecetes opilio* tagged and released in October, 1969 and May, 1970. All crabs were recaptured during the 1970 fishing season. Percentages are in parentheses (from Watson and Wells, 1972)

| Distance Travelled (in miles) | Release Location (Station Number)[1] | | | | | | | All Stations Combined | Stations 1 & 2 Only; Tagged 1969 | Stations 3, 4, 5, 8 & 9 Tagged 1970 |
	1	2	3	4	5	8	9			
<5	23 (31.1)	0 (0.00)	33 (27.5)	21 (25.3)	0 (0.0)	48 (100)	22 (47.8)	147 (33.7)	23 (25.0)	124 (36.4)
5 – 10	29 (39.2)	6 (33.3)	31 (25.8)	41 (49.4)	42 (95.5)	–	0 (0.0)	149 (33.8)	35 (38.0)	114 (33.4)
10 – 15	9 (12.2)	7 (38.9)	27 (22.5)	11 (13.2)	0 (0.0)	–	24 (52.2)	78 (18.9)	16 (17.4)	62 (18.2)
15 – 25	9 (12.2)	3 (16.7)	22 (18.3)	6 (7.2)	2 (4.5)	–	0 (0.0)	42 (9.7)	12 (13.0)	30 (8.8)
25 – 35	4 (5.3)	2 (11.1)	7 (5.9)	4 (4.9)	0 (0.0)	–	0 (0.0)	17 (3.9)	6 (6.6)	11 (3.2)
Total Returns	74	18	120	83	44	48	46	433	92	341

[1] Stations 6 and 7 were omitted because no information on movements was available.

APPENDICES

APPENDIX I

LARVAL DEVELOPMENT

Included in this section are taxonomic descriptions of the prezoea, zoea, and first instar of *Chionoecetes opilio* and related brachyurans.

I. THE PREZOEA OF *CHIONOECETES OPILIO*

"Prezoea of *C. opilio* are identical in all respects to those of *C. bairdi*. The prezoea (see Figure 2) has the following characteristics: Cuticle of antennules, antennae, and telson delicately plumed. Antennule (Figure 2c) has two projections, one appreciably shorter than the other; shorter projection nonplumose. Exopodite of antenna (Figure 2d) has four plumose projections; endopodite has a simple nonplumose projection, no projection arising from area of rudimentary flagellum. Endopodites and exopodites of first maxilliped (Figure I-1.G) and second maxilliped (Figure I-1.I) consists of simple sheaths. Telson (Figure 2e and f) has seven projections on each side; following Lebour (1928), these are numbered from the inside 1 to 7; fourth projection short and nonplumose and covers spine that in zoea forms tip of telson fork; seventh projection also nonplumose but may occasionally have a few hairs.

The average carapace length (50 specimens) is 0.39 mm (range 0.32 to 0.46 mm) and the average total body length is 2.48 mm (range 2.2 to 2.80 mm)" (Haynes, 1973). *C. bairdi* prezoea are identical (Figure I-2).

II. THE ZOEA I OF *CHIONOECETES OPILIO*

"General shape (Figure 4) characteristic of larvae of subfamily *Oregoniinae*. All spines well developed and armed with fine spinules on at least the distal half of their length. Dorsal and rostral spines long, tapering, and usually slightly "s" shaped; dorsal spine slightly longer than rostral. Lateral spines large; at right angles to carapace and curved downward slightly. Eyestalks short, not articulated, and each bears a minute protuberance about midway between eye and carapace. Carapace has slight medial crest with noticeable hump on front of head. Distinct protuberance on carapace posterior to dorsal spine. A minute hair on each side of carapace between lateral spine and base of dorsal spine. Total of six setae along posterior edge of carapace all arising from inner side of carapace; posterior three setae longer and stouter than anterior three setae. Lateral margin of carapace strongly indented just posterior to eye.

The averages for the following measurements (50 specimens) are: carapace length 0.54 mm (range 0.45 to 0.73 mm); dorsal-rostral

length 4.17 mm (range 3.96 to 4.55 mm); width between tips of lateral spines 2.73 mm. (range 2.52 to 2.97 mm); and total body length 5.15 mm (range 4.96 to 5.60 mm)" (Haynes, 1973).

Antennule (Figure 4b). "Antennule conical and uniramous, with five terminal processes -- three long aesthetes and two shorter setae; two aesthetes about equal in length, but third only slightly longer than longest setae" (Haynes, 1973).

Antennae (Figure 4b). "Protopodite (spinuous process) of antennae elongate; slightly shorter than rostral spine and armed with numerous sharp spinules that increase in size distally. Exopodite slender; less than half the length of protopodite; two setae near sharp tip, each with two rows of many fine setules. Endopodite (flagellum) rudimentary (represented by small protuberance near proximal end of protopodite)" (Haynes, 1973).

Mandibles (Figure I-1.B). "Mandibles without palps. Incisor composed of two large pointed processes. A subterminal denticle that arises from ventral side of mandible occurs on molar process of right mandible but not on left mandible" (Haynes, 1973).

Maxillule (Figure I-1.D). "Endopodite two segmented, with six setae on terminal segment (arranged in pairs, one pair being terminal) and one seta on distal end of basal segment. Basal endite bears seven setae at distal end (two setae are especially stout). A bluntly pointed projection one-eighth the height of nearest seta occurs between basal endite setae and endopodite. Coxal endite bears seven setae at distal end. All setae on maxillule plumose" (Haynes, 1973).

Maxilla (Figure I-1.F). "Maxilla bears large plate-like exopodite (scaphognathite) with 11 (rarely 12) lone, evenly spaced plumose setae along outer margin and one longer and thicker seta at proximal end. Endopodite only slightly bifurcate; bears many fine hairs along outer margin and three setae on each lobe. There are two endites, both slightly bifurcate; basal endite (distal) has five setae on each lobe. All setae sparsely plumose except those on exopodite, which are heavily plumose" (Haynes, 1973).

First Maxilliped (Figure I-1.H). "Exopodite appears to have two segments but segmentation not complete; four heavily plumose segmented (natatory) setae on distal end. Endopodite five segmented -- setation formula is 5, 2, 1, 2, 3. Basis has 10 setae along posterior edge -- setation formula is 3, 3, 2, 2. All setae except natatory setae sparsely plumose" (Haynes, 1973).

Second Maxilliped (Figure I-1.J). "Exopodite not completely segmented; four long, heavily plumose segmented (natatory) setae on distal end. Endopodite three segmented -- setation formula is 5, 1, 1. Basis has four setae along posterior edge. All setae except natatory setae sparsely plumose" (Haynes, 1973).

<u>Third Maxilliped.</u> "Developing third maxilliped small, rudimentary, and not segmented; tip bilobed" (Haynes, 1973).

<u>Pereiopods.</u> "Five developing pereiopods beneath carapace; they are small, rudimentary, and not segmented or bilobed" (Haynes, 1973).

<u>Abdomen and Telson</u> (Figure 4D). "Abdomen consists of five segments and telson (somite six is fused with telson in stage I). Each segment has pair of hairs near dorsal posterior margin; second and third segments both have pair of slightly curved lateral knobs -- pair on third segment about one-half the length of pair on second; pairs of long, well-developed spines, which become progressively shorter posteriorly, on posterior lateral margin of 3rd, 4th, and 5th segments; those on third barely extend beyond posterior margin of adjacent segment; those on fourth do not quite reach the posterior margin of the fifth segment; those on the fifth segment extend posteriorly to level of anus; lateral spines may or may not have few minute hairs. Telson bifurcate; furcations long, slender, and finely spinulate and have upcurved tips; each furcation bears three articulated telson setae on inner side, a prominent spine laterally on outer margin, a smaller dorsal spine posterior to telson setae, and a minute spinule about midway between the lateral and dorsal spines; lateral and dorsal spines on furcations minutely spinulate. Each telson seta has two rows of spinules, and each row has two types of spinules. First type short but wide at base, resembling row of "teeth"; second type small and hairlike; first type extends about three-fourths the length of the seta and decreases in size proximally; second type covers distal one-fourth of seta; spinules in both rows fit this description, although those on one row are considerably smaller than those on the other. Pleopods and uropods developing, but not evident at this stage" (Haynes, 1973).

III. THE INSTAR I OF *CHIONOECETES OPILIO*

"The general morphology (Figures 8 and 9) is similar to that of the adult, except the carapace. The carapace is flat and the rear of it is rather narrow to form a violin-like shape. (The surface of the carapace bears many wart-like structures composed of granules). The rostrum protrudes almost horizontally, and the rostral spines are pointed and well developed. Their tips are curved inward. The spines behind the eyes are well developed, but the middle spines are very small. The antennae are shorter than the forehead spines. The propodites of the cheliped are round and rather large, but all walking legs are slender and flat. The length of the longest propodites is as follows: cheliped 1.3 mm; the first leg 2.5 mm; the second leg 2.0 mm. The surfaces of the legs have short hairs except the propodite and dactyl. It was impossible to determine the sex of the samples of less than 6 mm carapace width in this study. The sex of instars over 6 to 7 mm in carapace width can be distinguished by their abdominal appearance as the secondary sex characteristics" (Ito, 1968).

Ten specimens of the Instar I stage, having carapace width range 2.6 to 2.9 mm (average 2.8 mm) and carapace length 3.6 to 4.0 mm (average 3.8 mm), were examined by Kon (1970) to provide the following description:

"The ratio of carapace length/carapace width is considerably greater in
first instars than in mature adults and the former show a marked difference
in the upper portion of the cardiac region. In particular, a pair of
frontal bristles with many serrations is well developed in the first instar.
These bristles protrude forward and are widely spaced. The 'eye sockets'
are vertically elongated and the frontal region, which they form, occupies
approximately one-third of the carapace length. Many small verrucae occur
on the frontal, occular, and stomach regions of the dorsal surface
of the carapace. An indistinct and dull pair of protuberances are
situated 'near the center of the edge of the dorsal shell' in the
megalops. The ventral portion of the cephalothorax and the entire
surface of the legs are covered with short hairs. The second
antennae are longer than the frontal bristles (Figure 8).

The specimen which was shown by Ito (1968) as the young of Tanner
crab of the first period differs from that of the author in the
following respects: that the former has no hair over the whole of
its body, and that its second antennae are extremely short. It looks
as though the differences are due to the fact that Ito's specimens
had been collected from the stomach of fish" (Kon, 1970).

(Data from: Haynes, E. 1973)

Species A	Species B
Distinguishing Characteristics of A	Distinguishing Characteristics of B

P R E Z O E A

C. bairdi

Virtually no difference (Figures 2 and I-2)

C. opilio and C. bairdi
The shorter embryonic spine of the antennule is nonplumose.

C. opilio

Virtually no difference

C. opilio elongatus
The shorter embryonic spine of the antennule is plumose.

Z O E A   S T A G E   I

C. bairdi

(1) Posterior lateral spines on 3rd and 4th abdominal segments overlap adjacent segments by about 1/3 the length of spines. (2) Especially in the area of the developing pleopods, the abdomen is slightly deeper.

C. bairdi and C. opilio

(1) Total body length 4.96 – 5.60mm (2) Antennule with 3 aesthetes and 2 setae. (3) Posterior lateral spines barely reach the posterior margin of the adjacent segment.

C. opilio and C. bairdi

(1) Lateral knobs on 3rd abdominal segment do not come close to posterior margin of the segment.
(2) Only 1 or 2, if any spinules on lateral abdominal spines
(3) Only 11 setae (rarely 12) along the outer margin of the exopodite of the maxilla in addition to the stout setae.

C. opilio

(1) Posterior lateral spines on 3rd segment barely extend past posterior margin of 4th segment those of 4th segment don't quite reach posterior margin of the 5th segment. (2) Abdomen is slightly more shallow.

Oregonia gracilis and Hyas lyratus

(1) Size only 1/2 that of *Chionoecetes*.
(2) Antennule with 2 aesthetes and 1 (or sometimes 2) setae. (3) Posterior lateral spines extend beyond the posterior margin of the adjacent segment about 1/3 the length of the spine.

C. opilio elongatus

(1) Lateral knobs on 3rd abdominal segment almost reach posterior margin of the segment.
(2) Posterior lateral spines on abdomen covered with spinules.
(3) Outer margin of the exopodite of maxilla with 15 setae in addition to the stout setae at the proximal end.

Z O E A   S T A G E S   I   A N D   II
(Data from Motoh, H. 1976)

C. opilio

Chromatopheres are brown or reddish.

C. japonicus

Chromatopheres are vermillion or crimson.

M E G A L O P S
(Data from Motoh, H. 1976)

C. opilio

Chromatopheres are brown or reddish. Length of the postero-lateral spine on the 3rd abdominal segment is shorter than (or barely equal to) the 4th abdominal segment. The ischiopodite of the cheliped has one spine.

C. japonicus

Chromatopheres are vermillion or crimson. Length of the postero-lateral spine on the 3rd abdominal segment is 1.3 times the length of the 4th abdominal segment. The ischiopodite of the cheliped is spineless.
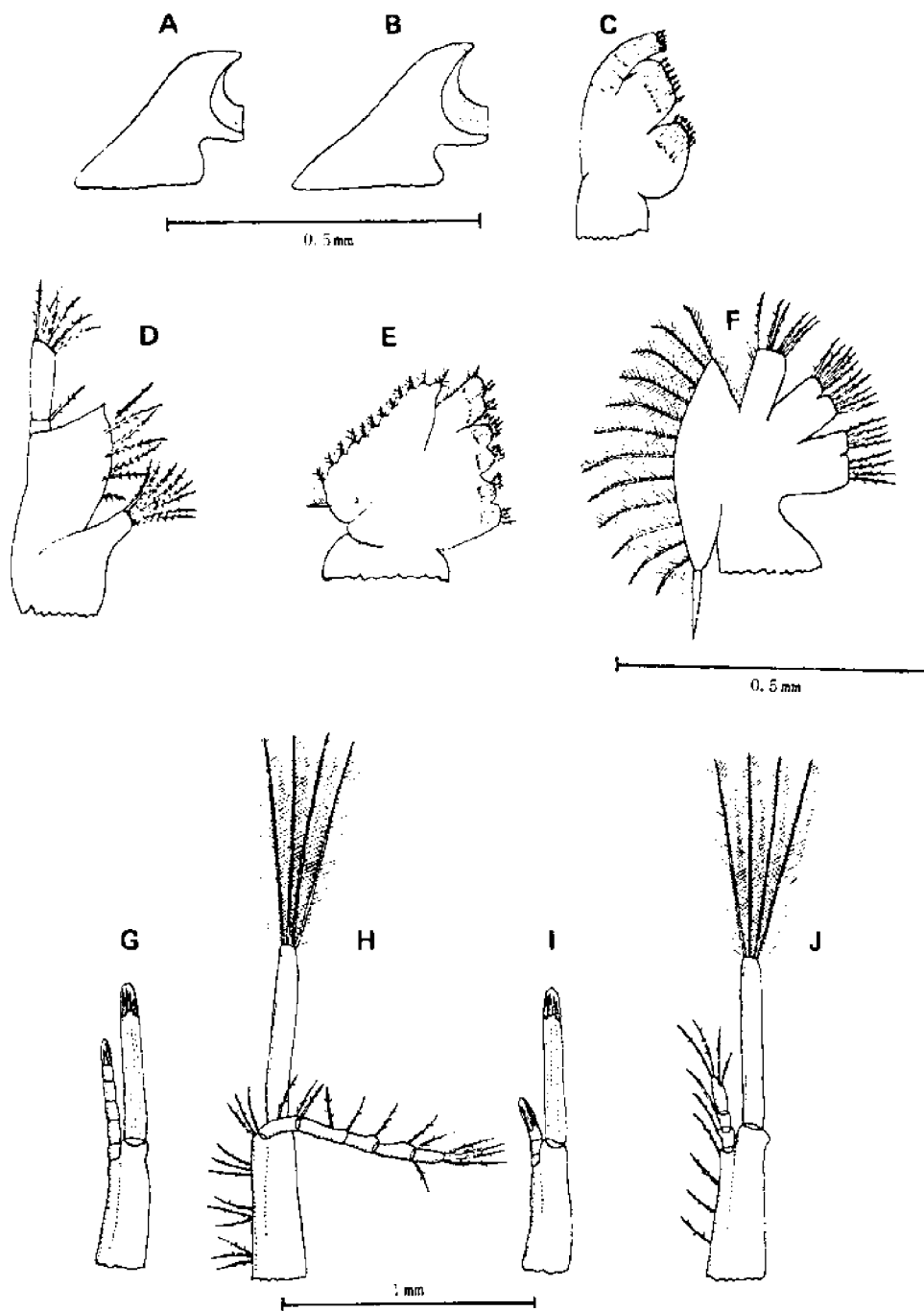
Figure I-1. Comparison of external features of prezoea and
zoea I of *Chionoecetes opilio elongatus* Rathbun.
A. Mandible of prezoea. B. Mandible of zoea I.
C. Maxillule of prezoea. D. Maxillule of zoea I.
E. Maxilla of prezoea. F. Maxilla of zoea I.
G. First maxilliped of prezoea. H. First maxilli-
ped of zoea I. I. Second maxilliped of prezoea.
J. Second maxilliped of zoea I (from Kuwatani et
al., 1971)
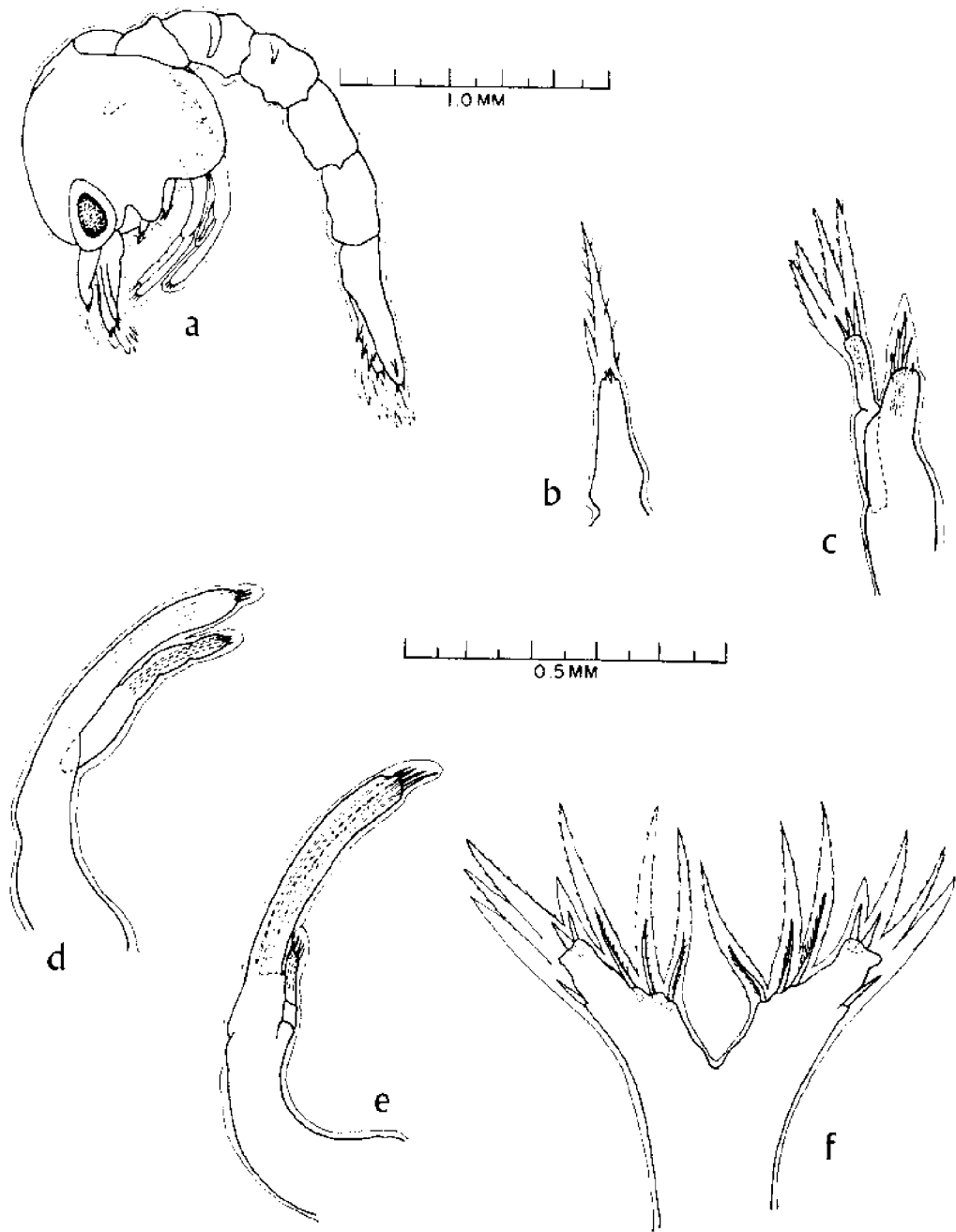
Figure I-2. (a) Prezoea of *Chionoecetes bairdi*, (b) antennule, (c) antenna, (d) first maxilliped, (e) second maxilliped, (f) telson (from Haynes, 1973)

APPENDIX II

RATES OF LARVAL DEVELOPMENT OF *C. OPILIO*

Researchers have sought estimates of the length of larval life of *C. opilio*
by two methods: (1) the observation of different larval forms in plankton
collections taken during different seasons; (2) the observation of larval
development in laboratory rearing experiments. Each author has had to make
certain assumptions to justify his estimates. The approaches, assumptions,
and estimates of each researcher are listed below:

A.   Kon, T. 1970.

(1)   The water temperature in the southwestern region of the
Japan Sea off Wakasa Bay at the time of hatching (February to
April) is shown in Figure 7. An examination of the figure
shows that down to 150 meters below the surface the tem-
perature remains in the range 11 to 13°C during February to
April and the thermocline occurs between 150 and 200 meters.
Assuming: (1) that *C. opilio* larvae hatch at the beginning
of February in Wakasa Bay; and (2) that they spend most of
the planktonic period at less than 150 meters, where the
temperature is 12°C, Kon (1970) utilized the laboratory
derived relationship between time required for molting and
water temperature to estimate the length of the planktonic
period.

In this case:

Predicted Length of Zoea I Stage $\approx$ 19.0 days at average
water temperature $= 12.0^{\circ}$C
Predicted Length of Zoea II Stage $\approx$ 20.4 days at average
water temperature $= 12.0^{\circ}$C
Predicted Length of Megalops Stage $\approx$ 27 days at average
water temperature $= 11.9^{\circ}$C

Predicted Total Planktonic Larval Period $\approx$ 66 days at
average water temperature $= 12.0^{\circ}$C

(2)   Kon's second estimation of larval period was based upon the
laboratory-derived relationship between the time required
for molting and the cumulative water temperature:

Avg. Cumulative Water Temperature $\approx$ 228 days$^{\circ}$C for Zoea I
Avg. Cumulative Water Temperature $\approx$ 241 days$^{\circ}$C for Zoea II
Avg. Cumulative Water Temperature $\approx$ 293 days$^{\circ}$C for Megalops

Total of Avg. Cumulative Water Temperatures $\approx$ 762 days$^{\circ}$C

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When the average water temperature = $12^{\circ}C$, the total larval
period will = 762 days$^{\circ}$C/ 12°C = 63 days.

Using the results of rearing experiments to support his opinion, Kon (1970)
firmly believes that the total larval period is completed in less than three
months.

>"...the present information is based on the assumption that the
>planktonic stages take place in depths less than 150 m, and that
>the period of low temperature between hatching and surfacing and
>the period when the megalops or young crabs of the first instar
>fall to the sea bottom was <u>not</u> regarded as important."

>"If one takes into consideration the fact that the results in the
>rearing experiments are not satisfactory (increased mortality
>occurs) at water temperatures less than 8°C, one may assume that
>the periods do not extend over a long interval as has been suggested
>in the past, and that they are less than three months even if one
>takes into account the period of low temperature from surfacing after
>hatching to sinking to the bottom."

B. Yamahora (1969) conducted laboratory rearing experiments in much the
same manner as Kon. From the cumulative temperature needed for each
molting stage and the estimated value of water temperature in the
natural environment Yamahora calculated the length of the first and
second zoeal states as 27 days each.

C. Similar rearing experiments by the Fukui Prefecture Marine Experiment
Station (1969) yielded estimates of 24 to 25 days each for the length
of zoea stages I and II. Assuming the water temperature in the natural
environment to be 10 to 11°C, they calculated a required period of 28
days for completion of the megalops stage.

D. Fukataki (1969) collected larvae of *C. opilio* (over much of the area
of the Japan Sea coast) in nets and from the stomachs of salmonids.
His estimate of the total planktonic period (between hatching and the
molt to the post-larval instar I) is 5 to 8 months. The zoea I and
zoea II stages are believed to last approximately one month apiece;
while the megalops stage is estimated to last approximately 3 months.

E. Ito (1970) upholds his estimation of a total larval period of 7 to 8
months (based on collections of larvae from the stomachs of
Petroschmidtia toyamaensis) with the following reasoning:

>"...if one takes into account the fact that the megalops move
><u>gradually</u> toward deeper water, and will spend their lives in
>the depths of 300 and 400 meters, and the fact that at this
>depth the water temperature is 1 to 3°C, then the length of
>the megalops can be estimated as between 9 and 10 months,
>even when the cumulative water temperature method of the
>Fukui Marine Experiment Station was used."

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Kon (1970) is somewhat skeptical of the results of his fellow workers for the following reasons: (1) Yamahora used rearing temperatures that were somewhat lower than the anticipated 11 to 13°C "natural temperature" range. (2) "... the inferences by Ito were indirectly based on materials which has been collected from the stomachs of fish, and no distinction was made between the larvae of Tanner crabs ("Zuwaigani" = *Chionoecetex opilio* and those of "Benizuwaigani" (red Tanner crabs) = (*Chionoecetes japonicus*), which were found in deeper regions."

THE METHODS OF ITO (1965 AND 1970) FOR DETERMINING CARAPACE HARDNESS AND MATURITY INDEX

In order to determine carapace hardness, Ito used Mokuya's Scale of Fruit Hardness (B-Model) with a maximum scale of 5 kilograms and calibrated in 0.1 kilogram units. This measurement was achieved by placing the pointed head of the scale at a right angle to the middle of the gastric region of the carapace and adding weight until the point pierced the carapace. "Since the maximum piercing weight measured by the scale was less than 4 kilograms, eight grades of 0.5 kilograms with the lowest Hardness 1 through the highest Hardness 8 were used."

The maturity index was calculated from the following formula:

$$\text{M.I.} = \frac{\text{Weight of Ovary (in grams)}}{\text{Body Weight (g.)} - \text{Weight of Attached Eggs (g.)}} \times 100\%$$

The maximum value was less than 12.0; therefore, twelve grades of 1.0 were established with the lowest value of M.I. = 1.0 and the highest value of M.I. = 11.

In his 1970 report, Ito frequently refers to two groups of female instars which he designated Group A and Group B females. Young, instar female crabs were assigned to either of these groups on the basis of ovarian development. The criteria are stated below:

(1) Group A = those female instars with ovaries in a condition of rapid maturation (M.I. = 2.1 or more).

(2) Group B = those female instars with the ovary in an immature condition (M.I. = 2.0 or less).

Ito (1965) conducted supplementary investigations of carapace hardness in the areas noted below:

Date of Investigation	Site of Investigation	225	240	250	260	275	300	350
				(in meters)				
May 7, 1965	The Sea of Japan: stations a straight line stretching N/E from Kumihama Harbor, Kyoto	+	+	+	-	-	+	+
May 14, 1965	The Sea of Japan: stations on a straight line stretching E/N from Takeno Harbor, Hyogo	+	+	+	-	+	+	-
May 18, 1965	The Sea of Japan: stations on a straight line stretching N/E from Hamasaka Harbor, Hyogo	+	+	+	+	-	+	-

Crabs that were collected in this study were grouped into the following categories:

SMALL: Those with carapace width <30 mm, both males and females.

MEDIUM: FEMALE: Carapace width >31 mm.
MALE: Carapace width measuring 31 to 70 mm.

LARGE: FEMALE: Included only mature specimens. The distinction between mature and immature individuals was based on physical features of the abdomen together with the presence or absence of external eggs.

MALE: Those with carapace width measuring over 71 mm. Since mature and immature males could not be easily distinguished on the basis of the physical features of the abdomen, Ito used the carapace width of immature females as a reference for determining maturity among males. Males with carapace width >71 mm were considered to be mature whereas those of carapace width $\leq$ 70 mm were considered to be immature.

The carapace width at maturity for males and females was nearly the same.

APPENDIX IV

DEPTH DISTRIBUTION AND HABITAT

In the main body of this paper, the depth distribution of *Chionoecetes opilio* was briefly discussed. This Appendix has been included to provide insight into Kon's (1969) study of depth distribution; his methods, results and conclusions.

Study Area and Duration and Sample Size

Specimens used in this report were collected from Wakasa Bay in Fukui Prefecture, Japan. During the first year of the study, November 1964–June 1965, samples were collected approximately once each month by trawling for one to two hours in each of the following depth zones: 175, 225, 275, 325, and 375 meters. In the second year, November 1965–June 1966, samples were collected once each month from 35 points chosen at random in the strata 225 to 375 meters. During the period November 1964–June 1965, 8,182 males and 4,577 females were collected. Sample sizes for the period November 1965–June 1966 were 8,518 males and 7,331 females. The author divided the depth distribution into five strata as shown below:

STRATUM NUMBER	I	II	III	IV	V
DEPTH	150–200 meters	200–250 meters	250–300 meters	300–350 meters	350–400 meters

Stratum #1 was omitted from the final analysis because only five crabs (of carapace width 18 to 41 mm) were taken in three trawling efforts in this stratum.

Discussion

Generally speaking, the highest number of crabs of both sexes were collected from the second stratum (200 to 250 mm). Below this stratum, the number of crabs decreased with increasing depth (Tables 32 and 33 and Figure 41). In most strata, males were more abundant than females, with the exception of the zone between 200 and 250 meters where females outnumbered males. In strata IV and V males outnumbered females by the ratio 6.0:1.6. Females were most abundant in strata II and III (200 to 250 meters and 250 to 300 meters).

Ito (1968) purports that instars live in "rather deep water." His supportive facts are as follows:

(1)   "Young crabs of the first, second, and third instar stages were collected for a long period (1963-1965) in water deeper than 260 meters."

(2) "...the number of young crabs eaten by each agogenge
(*Petroschmidtia toyamaensis*) ranged from a high value
of 0.84 at 325 meters to 0.52 at 350 meters, 0.45 at
300 meters, and 0.32 at 275 meters" (see Figure IV-1
and Table IV-1).

(3) "More small crabs of 7 to 10 mm in carapace width were
recognized at around 300 to 350 meters depth than in
shallow water" (as determined by trawl catches).

Ito (1968) concluded that the young settle to the sea floor at depths of 300
to 350 meters.

In Kon's (1969) study, mesh size of the trawl nets limited the smallest carapace
width of specimens to the sixth instar stage (15 to 20 mm carapace width). All
specimens belonging to the instar VI stage were collected in the 250 to 400 meter
depth zone. Taking into account Ito's (1968) estimation of depth distribution
at the time of settling and the limited migratory ability of the young, Kon
(1968) concluded that the first six instars on the sea floor remain near the
area of initial settling. A detailed description of depth distribution of the
older life stages is provided in the main body of the paper.

The main fishing zones for *C. opilio* are said to be 200 to 300 meters in depth
off the coast of the San-in district and in Wakasa Bay, 150 to 280 meters along
the Okhotsk coast of Hokkaido, and 30 to 60 meters in the Aniva Gulf off Sakhalin
(Kon, 1969). In the Gulf of St. Lawrence *C. opilio* is generally found at
depths between 40 and 250 meters (Table IV-2). Off Grande-Riviere, Quebec,
bottom temperature was between $-1^{\circ}C$ and $+5^{\circ}C$ in 45 out of 51 tows where the crabs
were found although some were caught in water as warm as $9.7^{\circ}C$ (Powles, 1966).

Substrate types in crab producing areas vary from mud to muddy sand to gravel
and rock. Mud appears to be the preferred substrate (Brunel 1960, 1961, 1962).

Powles (1966) states that the young of the species are probably more sensative
to environmental conditions and require a mud bottom whereas adults can move off
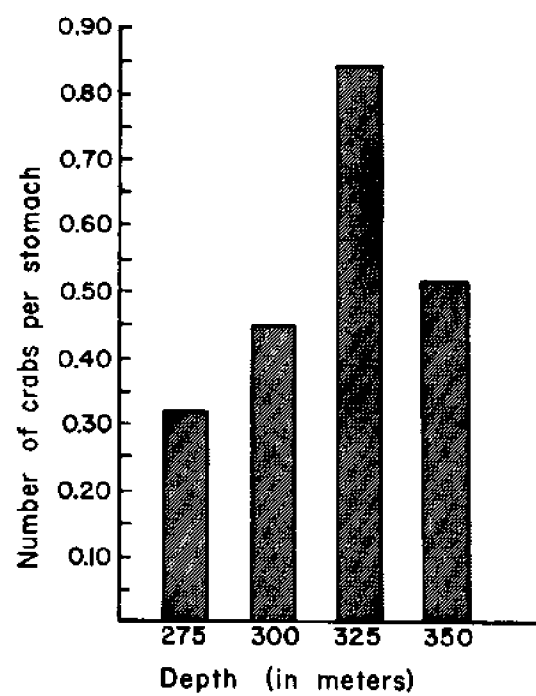the mud into areas of other sediment types.

Figure IV-1. Number of *Chionoecetes opilio* instars per zoarcid
stomach (*Petroschmidtia toyamaensis*) by depth
(based on data from Ito, 1968)

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Table IV-1. Number of instar *Chionoecetes opilio* eaten by the zoarcid, *Petroschmidtia toyamaensis*, by month and water depth (from Ito, 1968)

Number of zoarcids in column A
Number of *C. opilio* in all stomachs in column B
Average number of crabs per stomach in column C

Depth of Water	250 m			260 m			275 m			300 m			325 m			350 m			Total		
	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
1963																					
September	0	0	0	–	–	–	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0
October	0	0	0	–	–	–	0	0	0	0	0	0	0	0	0	18	5	0.3	18	5	0.3
November	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
December	0	0	0	–	–	–	0	0	0	1	0	0	0	0	0	5	0	0	6	0	0
1964																					
January	0	0	0	–	–	–	0	0	0	3	0	0	4	0	0	7	0	0	14	0	0
February	0	0	–	–	–	–	0	0	0	0	0	0	19	21	1.1	21	16	0.8	40	37	0.9
March	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
April	0	0	0	–	–	–	0	0	0	29	18	0.6	18	23	1.3	19	11	0.6	66	52	0.8
May	0	0	0	–	–	–	10	1	0.1	16	5	0.3	4	4	1.0	19	8	0.5	49	18	0.4
June	0	0	0	–	–	–	6	6	1.0	16	10	0.6	15	17	1.1	16	7	0.4	53	40	0.8
July	0	0	0	–	–	–	0	0	0	15	2	0.1	20	13	0.7	12	9	0.8	47	24	0.5
August	0	0	0	–	–	–	0	0	0	0	0	0	10	3	0.3	0	0	0	10	3	0.3
September	0	0	0	0	0	0	0	0	0	7	0	0	–	–	–	4	1	0.3	11	1	0.1
October	0	0	0	1	0	0	0	0	0	16	4	0.3	–	–	–	2	0	0	19	4	0.2
November	0	0	0	0	0	0	0	0	0	20	2	0.1	–	–	–	5	2	0.4	25	4	0.2
December	0	0	0	0	0	0	3	0	0	2	1	0.5	–	–	–	2	1	0.5	7	2	0.3
1965																					
January	0	0	0	0	0	0	3	0	0	5	0	0	–	–	–	13	5	0.4	21	5	0.2
February	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
March	0	0	0	0	0	0	12	5	0.4	20	10	0.5	–	–	–	6	5	0.8	38	20	0.5
April	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
May	1	0	0	1	0	0	4	0	0	31	33	1.1	–	–	–	18	16	0.9	55	49	0.9
TOTAL	1	0	0	2	0	0	38	12	0.3	181	85	0.5	93	81	0.8	165	86	0.5	480	264	0.6

Ito excluded the depths 175, 200, 225, and 240 meters because no zoarcids were caught in the corresponding tows.

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Table IV-2. Depth zones inhabited and substrates of crab producing areas in the Gulf of St. Lawrence

AUTHOR(S)	LOCATION	SUBSTRATE	DISTRIBUTION	MAJOR CONCENTRATIONS
Deveau and Aucion (1966)	Cape Breton Island (northern coast)	Rock or Gravel	65-200 m	90-180 m
Deveau and Aucion (1966)	Cape Breton Island (western coast)	Muddy Sand	65-200 m	90-180 m
Powles (1966)	Off Grande-Riviere, Quebec	---	120-200 m	---
Watson (1969)	Gulf of St. Lawrence	---	40-250 m	95-170 m

APPENDIX V

SEASONAL VARIATION IN WATER TEMPERATURES OF WAKASA BAY
ON THE SEA OF JAPAN AND CHALEUR BAY OF THE GULF OF ST. LAWRENCE
AND THEIR POSSIBLE EFFECT ON THE APPEARANCE OF THE LARVAE OF
CHIONOECETES OPILIO

The development and behavior of any organism is affected by extrinsic as well as intrinsic factors. Among those factors which influence a marine invertebrate's development and behavior, one might list such environmental variables as water temperature, specific gravity of water, and chlorinity. Still other factors (such as light, suspended sediments, availability of food, and contaminants) may be of greater or lesser importance; however, with respect to *Chionoecetes opilio*, the greatest amount of work has been done on suitable versus lethal temperature ranges. In the following paragraphs some consideration is given to the seasonal variations in water temperature as they relate to the appearance of different developmental stages of *C. opilio*.

The larvae of *C. opilio* are reported to hatch between February and April in Wakasa Bay (Ito, 1965). Assuming that berried females do occur at depths of 200 to 250 meters, as described by Japanese researchers, then water temperatures at the depth and time of hatching (in Wakasa Bay) are in the approximate range of 5° to $10^{O}C$ (Figure 7). If, as all studies seem to indicate, the free-swimming prezoeal stage lasts only a small fraction of one day then the appearance of first stage zoea should coincide with that of prezoea. First stage zoea have been collected from the surface waters of the Sea of Japan during the monthly interval of March through May (Fukataki, 1975b and Ito, Kasahara, and Ikehara, 1967).

Surface water temperatures during these months are in the range of 11 to $18^{O}C$ (Figure 7). Kon's (1970) laboratory rearing experiments indicate that suitable temperatures for the survival and growth of *C. opilio* zoea I and II are in the range 7 to $15^{O}C$. First stage zoea are collected when surface temperatures are 4 to $16^{O}C$, second stage zoea at 4 to $17^{O}C$, and megalops at 1 to $17^{O}C$ (Kon, 1970). Megalops appear in the Sea of Japan between April and June (Table 5). Surface water temperatures at that time are 11 to $23^{O}C$ in Wakasa Bay. Kon (1970) describes the suitable temperature range for survival and growth of *C. opilio* megalops as 12 to $17^{O}C$. It appears that the model of life history, natural occurrences of *C. opilio*, laboratory derived limits of tolerance, and temperature regime of the environment during each larval stage are in reasonable agreement.

In the Gulf of St. Lawrence, *C. opilio* occurs in water approximately 55 to 180 meters deep with the highest concentrations between 90 and 160 meters (Watson, 1969). If, as Watson suggests, very little migratory behavior is exhibited then it is very possible that the larvae hatch within areas bounded by the 200 m isobath. Hatching occurs in the area of the Gulf of St. Lawrence from late April to June (Watson, 1969). Temperatures at the depths inhabited by *C.*

opilio in Chaleur Bay during June are less than 0°C (Figures V-1 to V-3). Liberated larvae are encountered in the Gulf of St. Lawrence during the months of April through June (Watson, 1969). Surface water temperatures ranged between 1.2°C and 14.0°C in Chaleur Bay during these months in the years 1959-1962 (Figures V-4 to V-8). Apparently hatching occurs at lower temperatures in Chaleur Bay than in Wakasa Bay which suggests that the prezoea, zoea, and megalops are more tolerant of lower temperatures in Chaleur Bay. Differences in the temperature tolerances of the two forms of *C. opilio* may be a major factor in limiting their distribution and extent of geographic overlap.

8 June 1961   5 June 1962
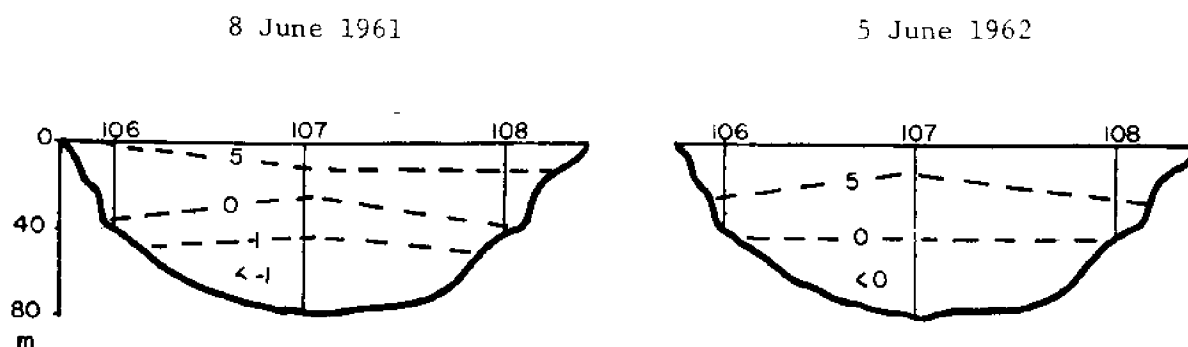
Figure V-1.   Isotherms along a transverse section from
                station 106 to 108 in the Bay of Chaleur
                (from Tiphane, 1963)

7 June 1961
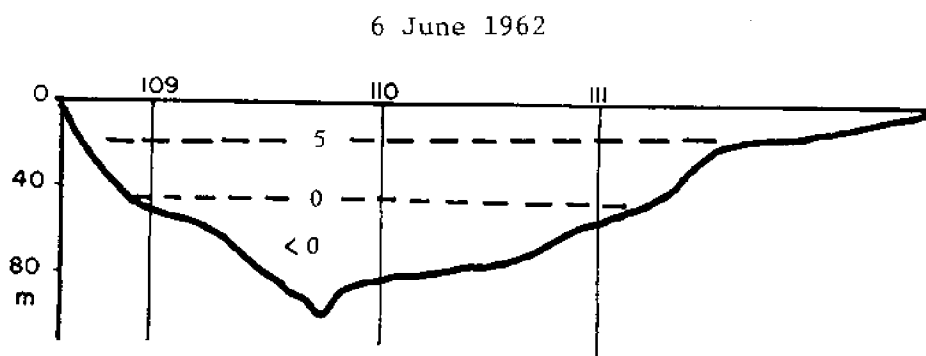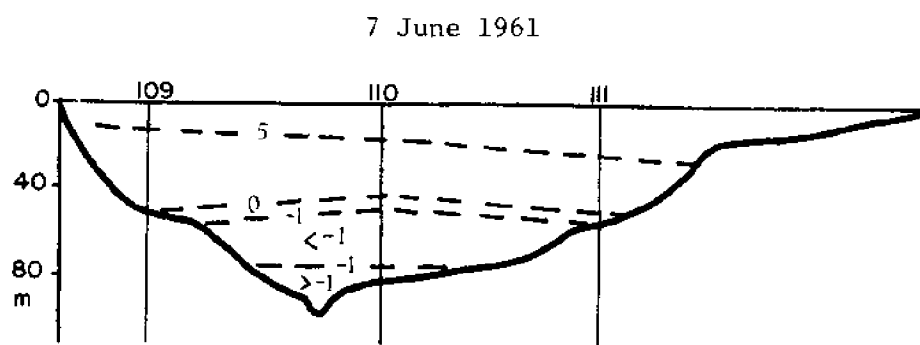
6 June 1962

Figure V-2.   Isotherms along a transverse section from
                station 109 to 111 in the Bay of Chaleur
                (from Tiphane, 1963)

126

10 June 1961
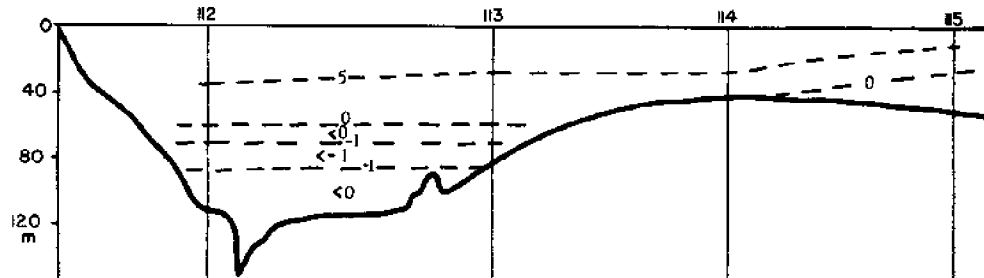
7 June 1962
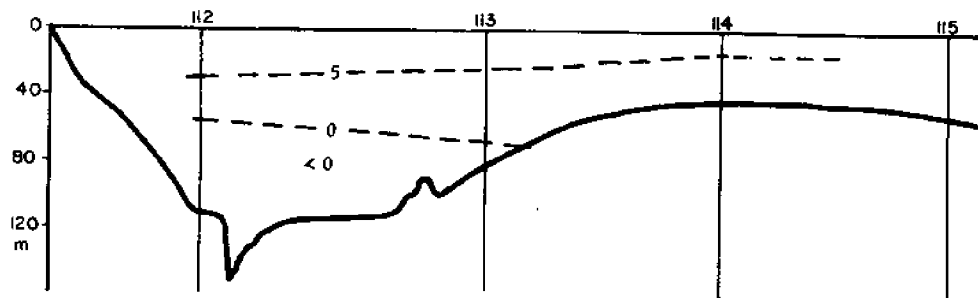
Figure V-3. Isotherms along a transverse section from
station 112 to 115 in the Bay of Chaleur
(from Tiphane, 1963)

127
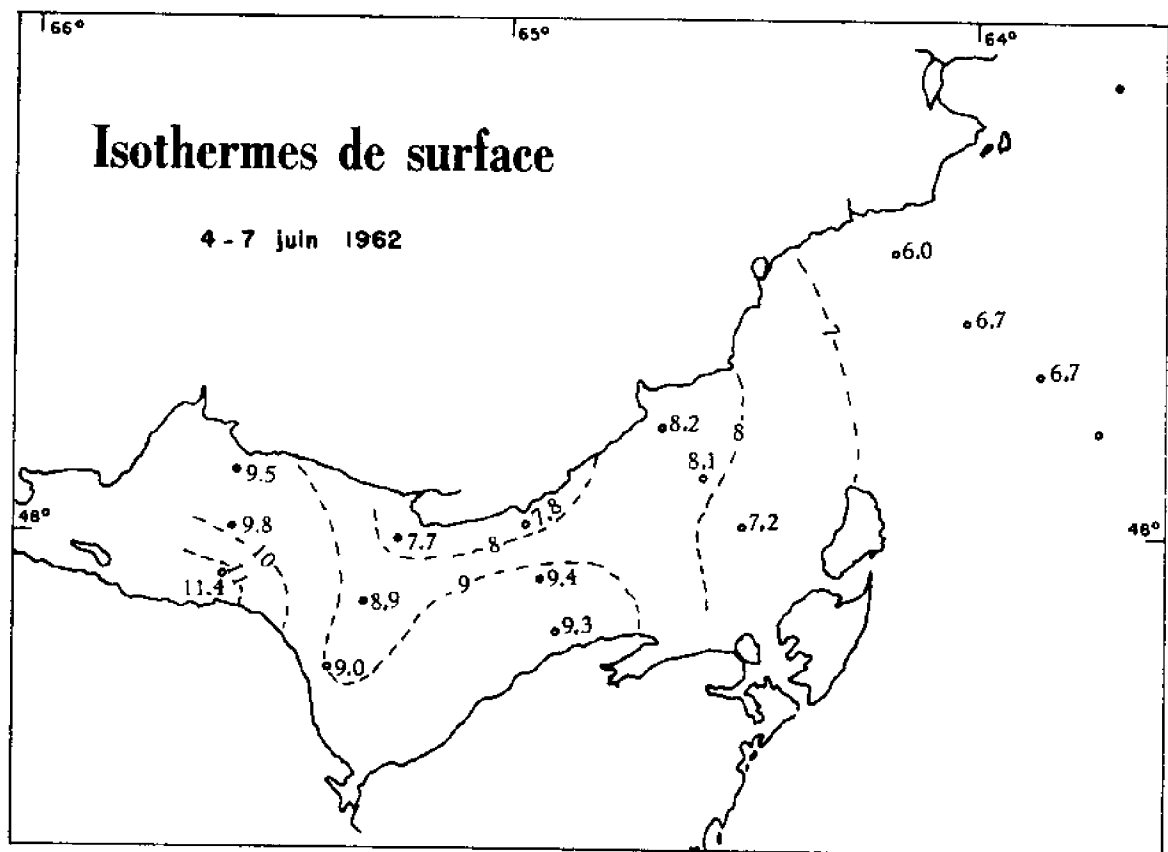
Figure V-4. Temperatures of the surface water recorded in
the Bay of Chaleur between 4 and 7 June, 1962
(from Tiphane, 1963)
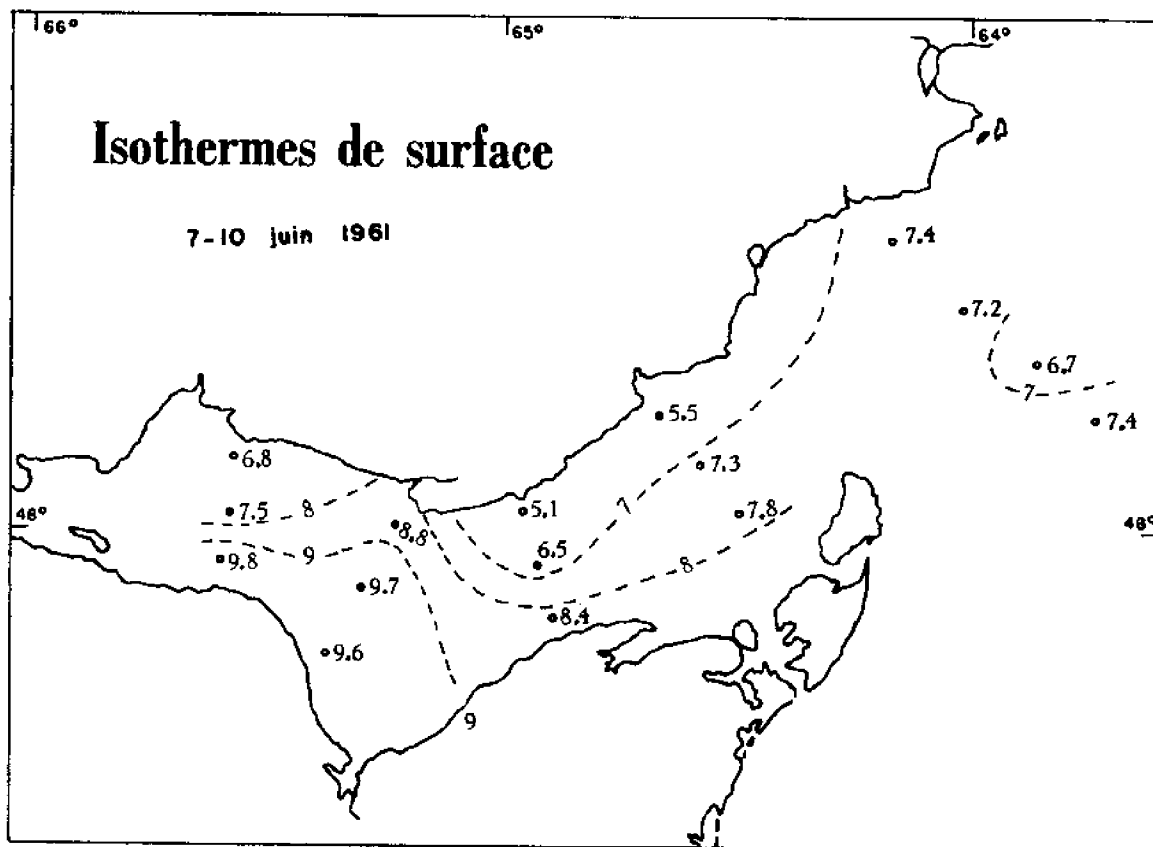
Figure V-5. Temperatures of surface water recorded in the
Bay of Chaleur between 7 and 10 June, 1969
(from Tiphane, 1963)

1959
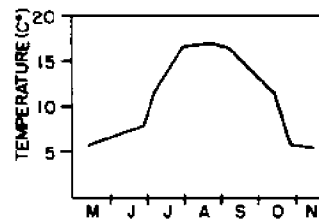
1960
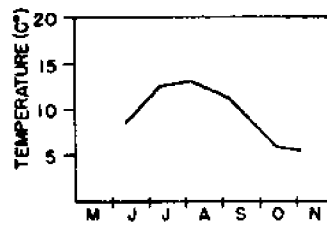
1961
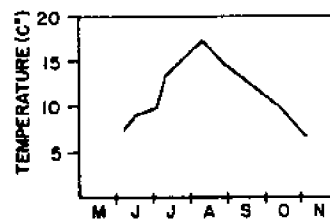
Figure V-6.   Seasonal variations in the surface temperature
at station 112 in the Bay of Chaleur during
1959, 1960, and 1961 (from Lacroix, 1962)
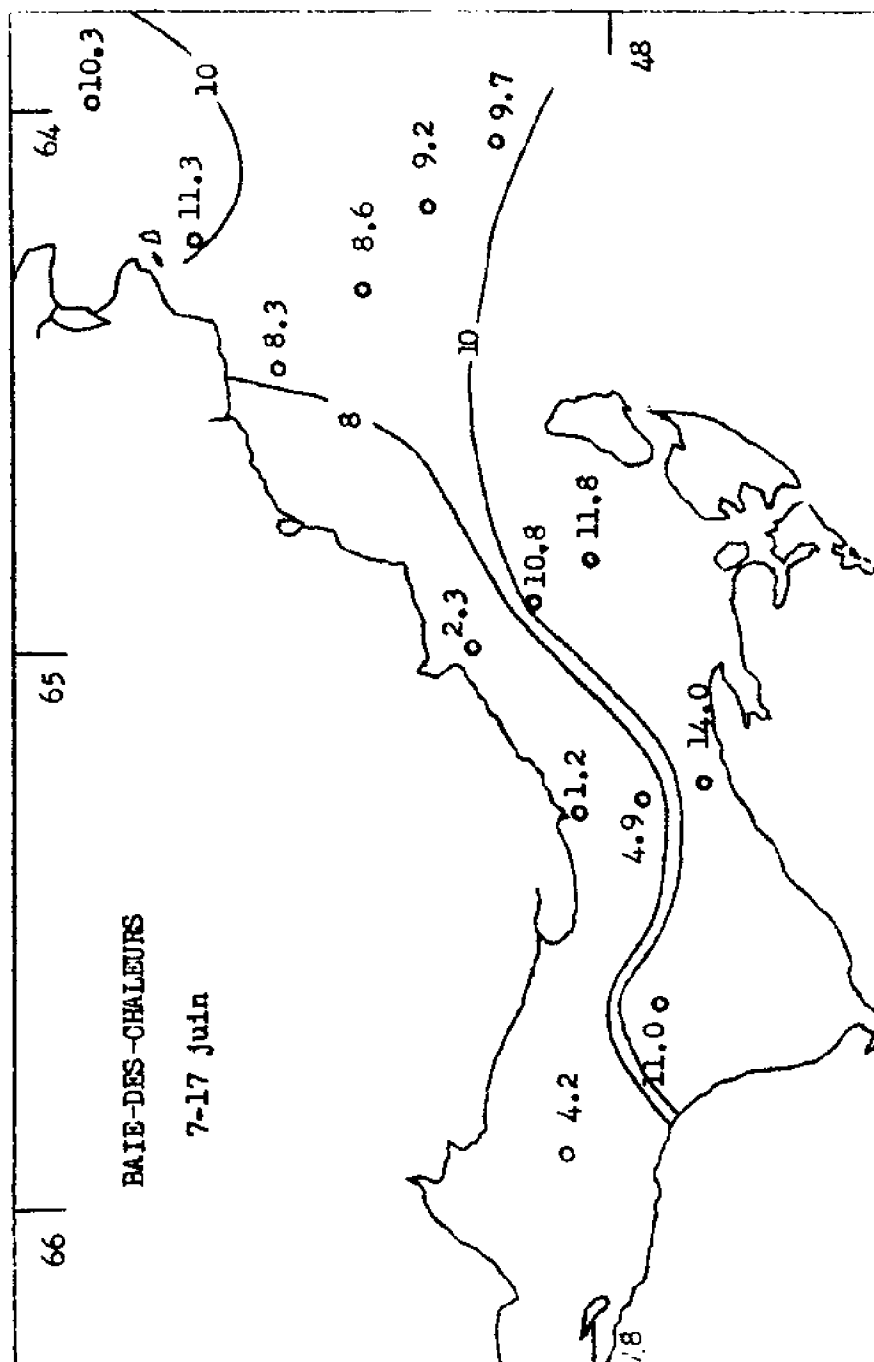
Figure V-7. Distribution of surface temperatures in June, 1960 (from Lacroix, 1961)

131
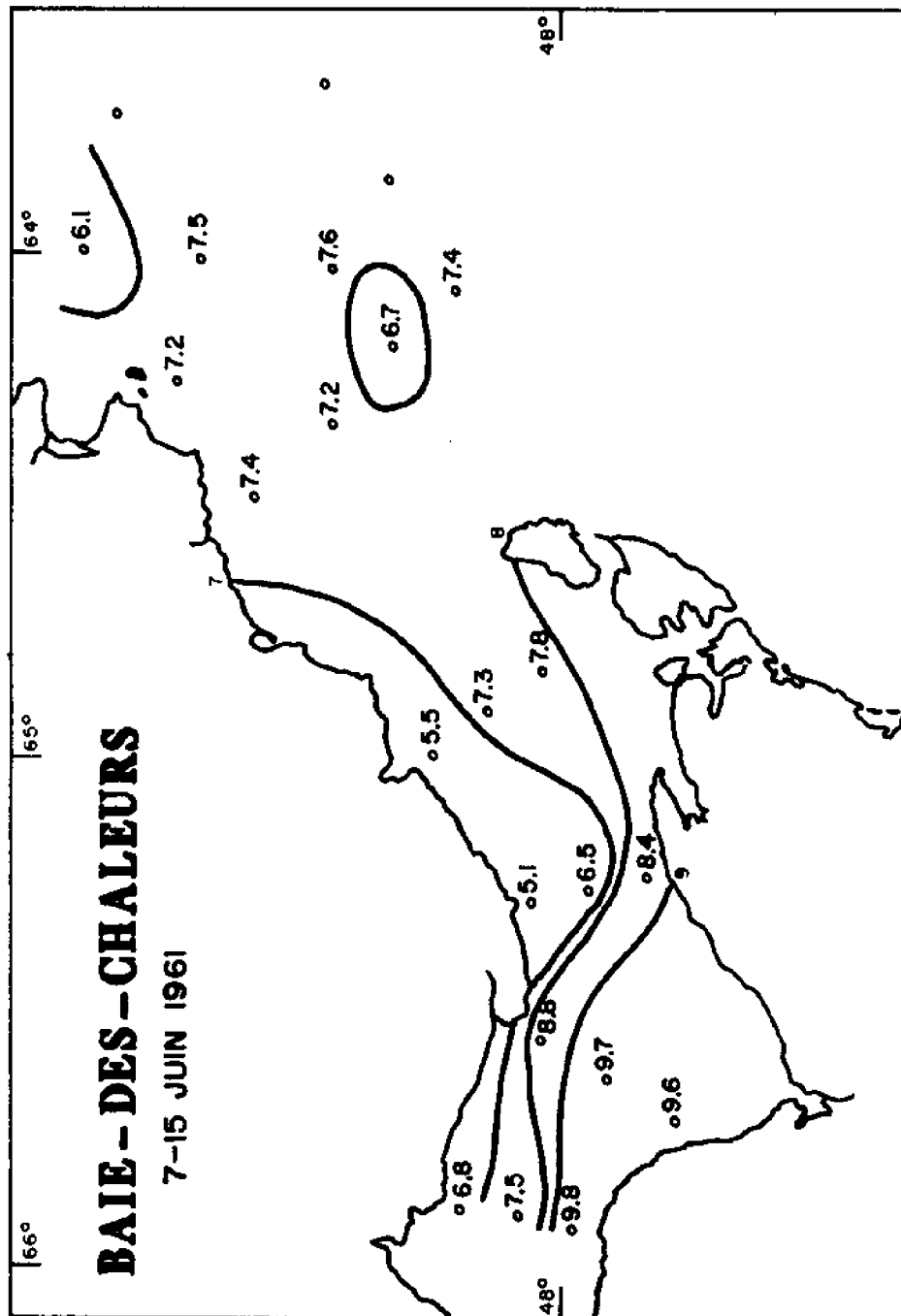
Figure V-8. Distribution of surface temperatures in June, 1961 (from Lacroix, 1961)

APPENDIX VI

THE FOOD HABITS OF *CHIONOECETES OPILIO*

No published data exist concerning the food habits of larval *C. opilio*; however, Paul, et al., (1978) described feeding responses of zoea I of the morphologically similar species *C. bairdi*. This study revealed that laboratory cultured zoea I suffered no mortality at prey concentrations equal to or exceeding 80 prey/liter, 20 percent mortality at concentrations of 40 prey/liter and 20 prey/liter, and 100 percent mortality in the absence of food (Paul, et al., 1978). Small copepods, copepodids, and copepod nauplii comprise the food of *C. bairdi* zoea and the authors noted that in the waters of the natural nursery area (kachemak Bay) prey densities were well below the laboratory optimum (Paul, et al., 1978). Assuming that *C. opilio* larvae also feed on small copepods then one might speculate that the extent of larval mortality may be greatly affected by the availability of these prey during the lengthy planktonic stage.

Dietary components of juvenile and adult *C. opilio* have been identified and quantified by Yasuda (1967) and Tarverdieva (1976). A total of 1,503 crabs with carapace width ranging from 18 to 150 mm were captured by Yasuda in Wakasa Bay during September 1964 and June 1965. Thirty species of animals, representing eleven classes and fourteen orders, and two species of plants were found in the stomach contents of these crabs (Yasuda, 1967). A systematic listing of the most important food items is given below:

Kingdom Animalia

Phylum Chordata
    Subphylum Vertebrata
        Class Osteichthyes

                Species   *Glyptocephalus stelleri*
                                 Arctoscopus japonicus
                                 Maurolicus japonicus

Phylum Echinodermata
    Class Ophiuroidea

                Species   *Ophiura paucisquama*

    Class Crinoidea
        Suborder Comatulidae
                Species   *Tropiometra aframacrodiscus*

    Class Holothuroidea
                Species   *Parastichopus nigripunctatus*

Phylum Arthropoda
    Subphylum Mandibulata
        Class Crustacea
            Subclass Malacostraca
                Order Decapoda
                    Suborder Reptantia
                        Species   *Chionoecetes opilio elongatus*

                    Suborder Natantia
                    Species   *Pandalus borealis*
                                    Nectocrangon ovifer
                                    N. lar

                Order Amphipoda
                    Species   *Pontoporeia sp.*

            Subclass Copepoda
                    Species   *Paracalanus sp.*
                                      Microsetella sp.
                                    Calanus sp.
                                    Oncaea sp.
                                    Candacia sp.

            Subclass Cirripedia
                    Family   *Balanidae sp.*

            Subclass Ostracoda
                    Species   *Cypris sp.*

Phylum Mollusca
    Class Pelecypoda
                    Species   *Portlandia pygmaea*
                                    P. japonica
                                  Nuculana robai
                                  Acila divaricata

    Class Gastropoda
                    Species   *Natica sp.*
                                    Buccinum striatissimum
                                  Neptunea intersculpta

    Class Scaphopoda
                    Species   *Euprynma morsei*
                                  Gonatus magister
                                  Wadasenia scintillans

Phylum Annelida
    Class Polychaeta
                    Species   *Aphrodite australis*
                                  Laetmatonice japonica

Phylum Protozoa
    Subphylum Sarcodina
        Order Foraminiferida
                    Species   *Globerigina bulloides*
                                  Cibicides lobatulus

Plant Kingdom

Phylum Chrysophyta
        Class Bacillariophyceae
                    Species   *Conscinodiscus wailessi*
                              C. radiatus

Yasuda (1967) concludes that the main food items are Ophiuroidea, Crustacea, and
Pelecypoda. Fish, Cephalopoda, Gastropoda, Scaphopoda, and Polychaeta are
commonly consumed. The plant species, the Cirripedia, and the Copepoda are in-
gested accidentally. The basic trophic pattern is that of an omnivorous scavenger.
This general trophic mode is confirmed by Tarverdieva (1976) who examined the
stomachs of 85 *C. opilio* from the southeastern Bering Sea. Tarverdieva (1976)
divided the crabs into three size groups and obtained the following results:
(A) The young (23 - 44 mm carapace width) fed "almost equally on crustaceans
(mainly amphipods), polychaetes (from the families Nereidae, Glyceridae, Phyl-
lodocidae, and the genus *Pectinaria*), and bivalves (*Nucula, Leda, Yoldia* and
from the family Ungulinidae). (B) Immature adult crabs (45 - 99 mm) mainly con-
sumed "...crustaceans (decapods - crabs, hermit crabs, and amphipods), worms
(genera *Sternaspis, Nephthys*, etc.), and to a lesser degree on bivalves and
brittle stars..."; however, the diversity of bivalves increased in this size
group. (C) Adults of commercial size (100$^+$ mm) fed primarily upon worms
(Polychaetes) although crustaceans (decapods), bivalves (*Yoldia hyperborea,
Nucula, Leda,* and *Spisula*), and brittle stars were also important dietary
constituents.

Tarverdieva (1976) expanded the list of prey observed by Yasuda (1967) with
the addition of the following animals:

                Phylum Porifera
                Phylum Coelenterata
                        Class Hydrozoa
                Phylum Bryozoa
                Phylum Pogonophora
                Phylum Arthropoda
                        Class Crustacea
                                Order Cumacea
                                Order Euphausiacea
                                Order Mysidacea

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APPENDIX E

Other Sources of Information

For additional information, a short bibliography of related publications follows.

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